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Miscellanea

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Observations on *Cycloclypeus (Cycloclypeus)* Carpenter and *Cycloclypeus (Katacycloclypeus)* Tan (Foraminiferida)

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Synopsis

Cycloclypeus carpenteri Brady and *C. guembelianus* Brady are redescribed from syntypic material and the former is considered to be a subjective senior synomym of the latter. The type species of *Cycloclypeus*, *C. mammillatus* Carter, is discussed and the type sample redated as Late Oligocene. It is concluded that this name should be allowed to lapse and that *C. carpenteri* should be declared the type species of the genus. *C.* (*Katacycloclypeus*) *annulatus* Martin is redescribed from syntypic material and compared with other katacycloclypeids occurring in Indonesia, and with the largest-known cycloclypeids from the Futuna Limestone of Fiji. It is considered that only one species of *Katacycloclypeus* can be recognized at present.

Introduction

The genus *Cycloclypeus* has long been recognized as having considerable stratigraphical value in the late Cenozoic owing to the relative ease with which the evolution of the early or juvenile part of the shell (embryonic and nepionic chambers: see Fig. 1) can be traced. Tan (1932) published the first detailed account of its evolutionary history and in so doing established it as a prime example of Haeckel's Law of Recapitulation. Although subsequent authors (Cosijn 1938, Drooger 1955 and MacGillavry 1962) have disputed and, indeed, disproved certain of Tan's conclusions, his main thesis – that after its initial appearance, the genus underwent a progressive shortening of the initial coil (so-called nepionic acceleration) through the reduction of the operculinoid and heterosteginoid stages – has never been questioned.

The purpose of this paper is to clear up some of the taxonomic confusion surrounding the living representatives of the genus and to describe *Katacycloclypeus* from the type section of the Futuna Limestone, Vanua Mbalavu, Fiji, where its association with planktonic foraminifera and *Lepidocyclina* makes it especially important for regional correlation.

The early growth stages of *Cycloclypeus* are illustrated and labelled in Fig. 1, and it is here necessary only to comment briefly on the stolon system and annuli. Stolons are pores which connect the secondary chamberlets through the primary septa. Because the septa are fairly thick, these pores appear as short tubes. As Carpenter (1856) discovered, each secondary chamberlet possesses two stolons on the distal wall, one opening on either side of the proximal end of each secondary septum in the succeeding annulus; Hottinger (1977) has described this arrangement as 'crosswise-oblique', and so far as is known this simple pattern is constant throughout the genus.

The term annulus has been used rather loosely in the past and has been a source of some confusion. Annulate cycloclypeids possess one or more rings of raised shell material between the centre of the test and the periphery (see Fig. 12). The annuli are composed of pillars which may be elevated above the test surface to form granules or pustules. When secondary shell material is laid down between the pustules, the annulus forms a thickened ring which may, or may not, show signs of external granulation. Thin sections, however, invariably show the presence of pillars in the wall. The area between two annuli is relatively depressed, as is the region between the inner annulus and the central boss when this is developed.

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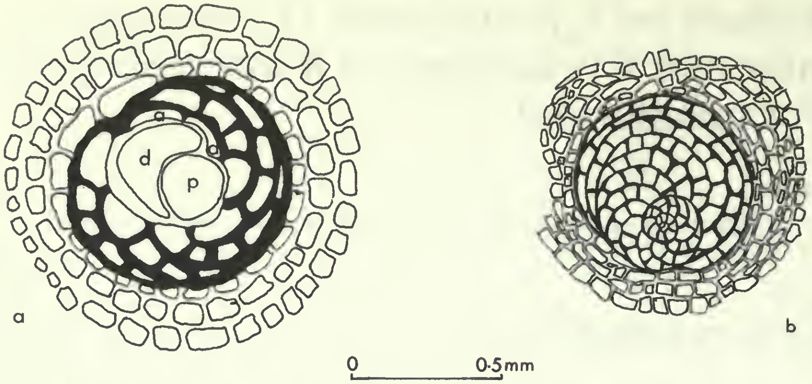

Fig. 1a, b. Early growth stages of megalospheric and microspheric forms of *Cycloclypeus* to illustrate the terminology used in this paper. Fig. a, megalospheric individual of *C.* (*C.*) *posteidae* Tan from the Futuna Limestone, Vanua Mbalavu, Fiji. The embryonic apparatus comprises the protoconch 'p' and deuterconch 'd'. The nepionic stage, outlined in black, includes an ana-nepionic chamber 'a' (in this specimen divided by a single septum but frequently undivided) and 5 nepionic chambers. The neanic stage is represented by the three rings of annular chambers which are divided into chamberlets by numerous secondary septa. Fig. b, microspheric individual of *C.* (*Katacycloclypeus*) *annulatus* Martin. Topotype; ex Martin Collection, Java. P.36377. See Fig. 9 for the internal structure of *C.* (*Cycloclypeus*) *carpenteri* Brady. The embryonic apparatus is invariably minute (c.20 μm) in the microspheric form. It is followed in this specimen by 8 undivided (operculinoid) chambers and at least 17 divided (heterosteginoid) chambers before the first annular chamber appears. As this specimen shows, it can be quite difficult to decide which is the first truly annular chamber.

The difference between *Cycloclypeus* and *Katacycloclypeus* is that the latter always possesses well-developed annuli in both generations, whereas the former usually lacks them. They may, however, be developed (usually feebly) in microspheric forms of *C. carpenteri* (Figs 2a, 4a, 5). The megalospheric forms of *C. eidae* and *C. posteidae* occasionally possess a single prominent annulus.

Acknowledgements

We are grateful to Mr Darwin Kadar (Geological Survey of Indonesia) for helpful information, and to Mr L. O'Herne (Rijksmuseum, Leiden) for kindly answering our numerous enquiries,

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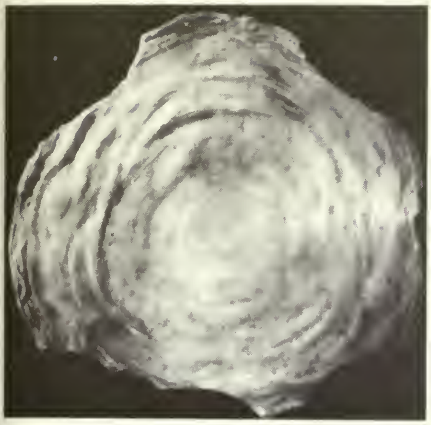
Figs 2a, b, 4a, b. *Cycloclypeus carpenteri* Brady. Microspheric forms (syntypes) from the Sir Edward Belcher Collection. 51.1.20.42, 43. Figs 2a, 4a, ×1. Note presence of incipient annuli towards periphery. Figs 2b, 4b enlargements (c. ×100) of part of shell to show the presence of granules along the primary septa (Fig. 4b) and along and between the septa (Fig. 2b).

Fig. 3. *Cycloclypeus posteidae* Tan, ×9. Heavily ornamented form (probably megalospheric) from sample F 181, Futuna Limestone, Vanua Mbalavu, Fiji. For internal details of this species see Fig. 1a.

Figs 5a, b. *Cycloclypeus carpenteri* Brady. Broken microspheric form from the Sir Edward Belcher Collection, Macclesfield Bank, 30 fathoms (=55 m), China Sea. Fig. 5a, ×1; Fig. 5b, enlargement of central area, c. ×4. Note development of annuli in the central area and compare with Figs 12–14 and 16. (1893.8.10.1).

Figs 6a, b. *Cycloclypeus carpenteri* Brady. One of three megalospheric forms in the Sir Edward Belcher Collection. This specimen possesses a multi-embryonic apparatus. Fig. 6a, ×2·8; Fig. 6b, central area (c. ×7) showing well-developed rings of granules on the primary septa and interstitial calcite largely obscuring the ornament over the central boss. 51.1.20.39.

Fig. 7. *Cycloclypeus carpenteri* Brady, ×20. Immature megalospheric form from '210 fathoms (=384 m) off Kandavu, Fiji'. This is Brady's (1881, 1884) unfigured syntype of *C. guembelianus*. Small granules of calcite can be seen on the raised central area. See Fig. 11 for details of internal structure. 1959.5.5.311.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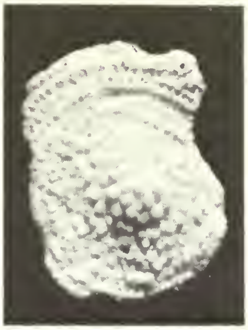
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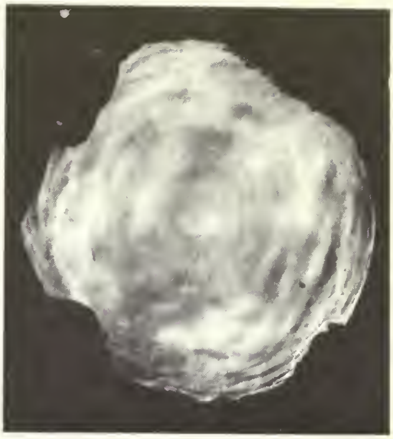
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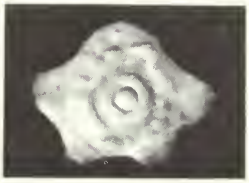
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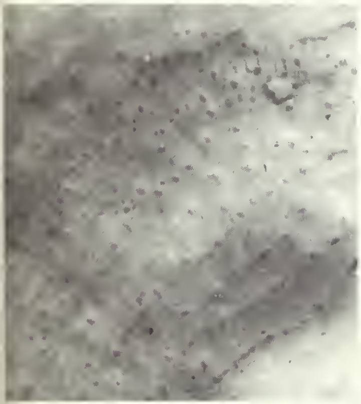
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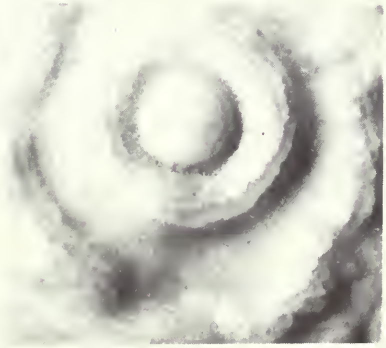
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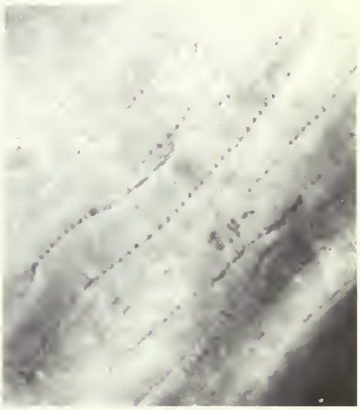
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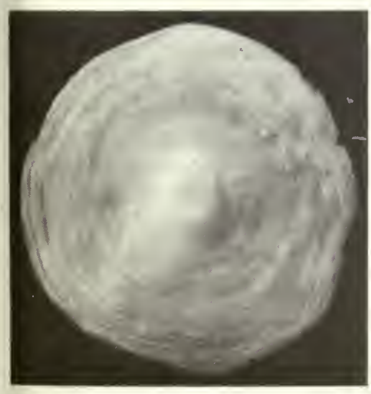
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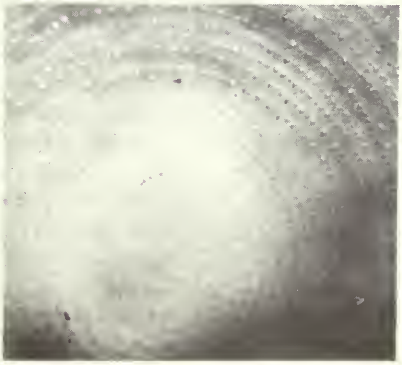
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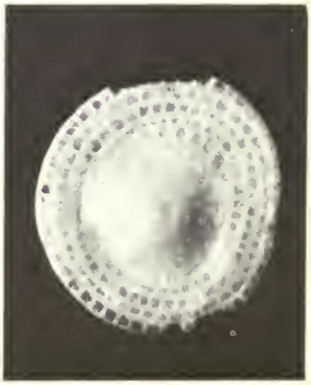
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loaning us comparative material, and allowing us to section one of Dr K. Martin's original rock samples from Java. We also wish to thank Miss Christine Harrison and Mr R. L. Hodgkinson for technical assistance, and Dr J. E. Whittaker for his careful reading of the typescript.

Material

Unless otherwise stated, all specimens figured or referred to herein are preserved in the British Museum (Natural History), and bear register numbers in the Palaeontological or Zoological collections which, although catalogued separately, are curated together.

Systematics

Family **NUMMULITIDAE** de Blainville, 1825

Genus ***CYCLOCLYPEUS*** Carpenter, 1856

Subgenus ***CYCLOCLYPEUS*** Carpenter, 1856

TYPE SPECIES. *Cycloclypeus mammillatus* Carter, 1861a.

Cycloclypeus was originally described from material dredged from 'water of a considerable depth off the coast of Borneo'. Carpenter obtained a number of specimens from the Belcher Collection in the British Museum and prepared some thin sections. He stated, somewhat ambiguously, that they were 'no less than 2¼″ (=57 mm) in diameter', and showed, amongst other things, that they had raised centres, pustulate surfaces and numerous complete or incomplete annuli. There are, in fact, three large specimens (57 mm, 50 mm and 48 mm in diameter respectively) in the original collection. We now know that they are all microspheric individuals. Although Carpenter described the microspheric generation, his figures were of one monstrosity (1856 : pl. 30, fig. 3; probably megalospheric) and one normal megalospheric individual (pl. 30, fig. 1) with a diameter of about 14 mm and a large proloculus. Unfortunately, no specific name was erected, the first validly described species being *C. mammillatus* Carter, 1861a, from Takah, south-east Arabia. According to the *Catalogue of Foraminifera* (Ellis & Messina 1940 *et seqq.*) it was said to be of Eocene age although Carter himself (1861a : 83) seemed uncertain. Thus, when Brady (1881 : 67) proposed that Carpenter's specimens should be named *C. carpenteri*, he was already too late to ensure that this became the type species of the genus.

Cycloclypeus **(*C.*)** ***mammillatus*** Carter, 1861

1861a *Cycloclypeus mammillatus* Carter : 87.
1861b *Cycloclypeus mammillatus* Carter : 461.

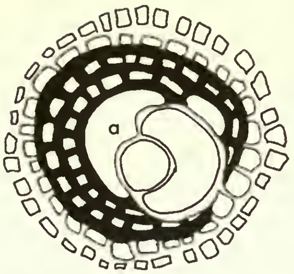
REMARKS. The single unfigured specimen on which this species is based has, unfortunately, been lost. However, the limestone sample whence it came is preserved in this Museum and has now been sectioned. Although Carter believed that he was dealing with an Eocene species, the newly-prepared thin sections reveal that the rock contains *Lepidocyclina* (*Eulepidina*) sp., *L.* (*Nephrolepidina*) sp. indet. (a small primitive form with rhombic equatorial chambers), *Heterostegina* sp. cf. *Heterostegina borneeensis* van der Vlerk and *Cycloclypeus* ex gr. *eidae* Tan (one specimen only). In the absence of any species of *Nummulites*, this assemblage clearly indicates a Late Oligocene age (Te_{1-4} in terms of the East Indies letter classification of the Tertiary; Adams 1970).

Since *C. mammillatus* was described from a single specimen and cannot be redescribed from the original material, we believe that the name should be allowed to fall into disuse, and that the ICZN should declare *C. carpenteri* to be the type species. An appropriate application has, therefore, been submitted to the Commission.

Cycloclypeus **(*C.*)** ***carpenteri*** Brady, 1881

Figs 2, 4–11

1856 *Cycloclypeus* Carpenter : 555; pl. 30, figs 1, 3, 4.
1862 *Cycloclypeus* Carpenter : 292; pl. 19, figs 2–7.



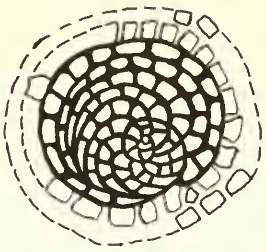
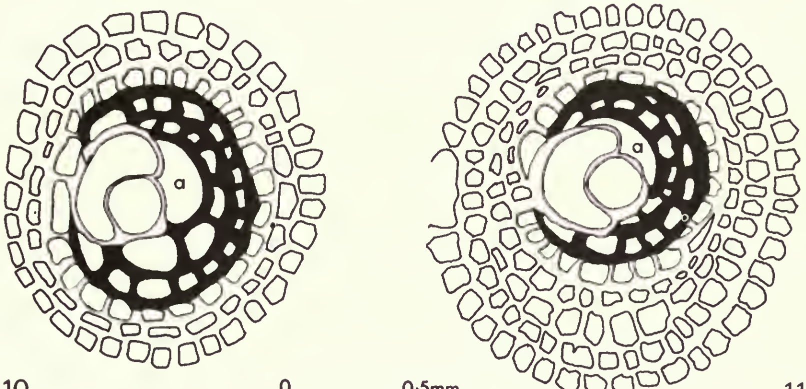


Fig. 8. *C. carpenteri* Brady. Megalospheric individual showing a large subdivided ana-nepionic chamber 'a' and 2 nepionic chambers. The external appearance of this specimen was illustrated by Chapman (1900 : pl. 3, fig. 4). 03.2.5.115.

Fig. 9. *C. carpenteri* Brady. Microspheric individual from Funafuti Atoll showing 4 operculinoid and 14 heterosteginoid chambers making up the nepionic stage. 03.2.4.951–1000 (sq. 49). Cf. the microspheric form of *C.* (*K.*) *annulatus*, Fig. 1b.



Figs 10, 11. Internal structures of the two complete syntypes of *C. guembelianus* Brady. Fig. 10 is the specimen illustrated (external view only) by Brady (1884 : pl. 111, fig. 8 a, b). Both specimens have one undivided ana-nepionic chamber, 'a'. Fig. 10 shows two nepionic chambers and Fig. 11 at least two nepionic chambers, but in this specimen it is difficult to decide at what point the first complete annular chamber begins. Fig. 10, ZF1366; Fig. 11, 1959.5.5.311.

1881	*Cycloclypeus guembeliana* Brady : 66
1881	*Cycloclypeus carpenteri* Brady : 67.
1884	*Cycloclypeus guembelianus* Brady : 751; pl. 111, fig. 8a, b.
1884	*Cycloclypeus carpenteri* Brady : 752.
1895	*Cycloclypeus carpenteri* Brady; Lister : 437, figs 52–54.
1900	*Cycloclypeus carpenteri* Brady; Chapman : 22; pl. 2, figs 6, 7; pl. 3, figs 1–5.
1927	*Cycloclypeus carpenteri* Brady; Hofker : 71; pl. 24, fig. 1; pl. 37, figs 1–10; pl. 38, figs 1–9, 12, 13.
1951	*Cycloclypeus guembelianus* Brady; Hanzawa : 1; pl. 1, figs 1–5; pl. 2, figs 1–7; text-figs 1–10.

REMARKS. Early descriptions of this species are confusing because authors have not distinguished between megalospheric and microspheric forms and because Brady's original description of *C. guembelianus* was inaccurate. The following brief descriptions are based upon Brady's syntypes, supplemented, where necessary, by specimens from Chapman's large collection from Funafuti Atoll. They are intended to distinguish clearly between the A and B generations, and between *C. guembelianus* and *C. carpenteri* as originally described.

Megalospheric generation (=A form) of *C. carpenteri* s.s.
Figs 6a, b, 8

MATERIAL. Three syntypes in the Belcher Collection, referred to by Carpenter (1856, 1862). A further 131 specimens, of which 6 have been sectioned, from Funafuti Atoll (Chapman 1900) have also been examined.

DESCRIPTION. The three well-grown syntypes (1 sectioned) range in diameter from 13 to 15 mm. All are ornamented by concentric rings of pustules which, except over the central area, arise from the junctions of the secondary and primary septa; these are broadest over the raised central boss where they are rather difficult to see owing to the presence of secondary shell material. The specimen (Fig. 6a, b) proved on sectioning to be abnormal in that it comprised 3 megalospheric embryonts having proloculus diameters of about 200 μm, 250 μm and 300 μm respectively. There is one other probable megalospheric specimen, one of the two monstrosities mentioned by Carpenter (1856 : 560). This appears to have developed from two megalospheric embryonts which grew their fused tests at right angles.

Chapman's large collection (155 specimens) from Funafuti Atoll contains 131 individuals that are indistinguishable externally from Brady's syntypes except insofar as they include a considerable number of small, immature individuals. Test diameter 1–13 mm (8–13 mm if obvious juveniles are excluded). Ornament is as described above. The six sectioned individuals have proloculi ranging from 190 to 280 μm in internal diameter followed by one ana-nepionic chamber and 1–3 (or ? 4) nepionic chambers. Even the smallest specimens (1–3 mm) are pustulate externally.

Megalospheric generation of *C. guembelianus* s.s.
Figs 7, 10, 11

MATERIAL. Two complete and one fragmentary specimens from 210 fathoms (= 388 m) off Kandavu, Fiji. Challenger Collection.

DESCRIPTION. The complete specimens have diameters of 1·5 and 2·0 mm respectively. In the smaller of the two specimens the proloculus has an internal diameter of 200 μm, and this is followed by a reniform second chamber (diameter 370 μm), one ana-nepionic and two nepionic chambers. Five neanic chambers are present. The second specimen has a proloculus diameter of about 190 μm, a second chamber with a width of 360 μm, one ana-nepionic and at least two nepionic chambers. At least four annular chambers are present. The early neanic chambers are shorter (radially) than wide. Contrary to Brady's second description (1884 : 751) the surface of the test is not smooth except for 'slightly raised lines' marking the annular and radial sutures, but is ornamented by small, irregularly-arranged pustules over the inflated embryonic apparatus. On one specimen the pustules are numerous and heavy.

Five other specimens of *C. guembelianus* in the Heron-Allen & Earland collection (Macassar Straits, 45 fathoms (=82 m)) differ little from Brady's specimens. They range 0·75–3·0 mm in diameter. All have one ana-nepionic and 2–6 nepionic chambers. Proloculus diameter ranges from 120 to 230 μm.

COMMENTARY. Brady (1884) stated that *C. guembelianus* was much smaller than *C. carpenteri*, but failed to realize that he was comparing immature megalospheric individuals with mature microspheric specimens. The discrepancy in size is therefore irrelevant. The only other difference noted by Brady was that the former was smooth and the latter highly pustulate. However, as noted above, the syntypes of *C. guembelianus* are not smooth; in fact they closely resemble the immature specimens of *C. carpenteri* from Funafuti. Young individuals of *C. carpenteri* have very delicate tests in which the large embryonic apparatus projects well above the surface of the equatorial chambers. As growth proceeds, the animal thickens the upper and lower surfaces of the shell with layers of calcite which are laid down around the primary pustules on the central area (Figs 6b, 7).

Later, the central area becomes smooth and domed, the pustules being arranged in concentric rings over the brim.

Microspheric generation (=B form) of *C.* (*C.*) *carpenteri*

Figs 2, 4, 5, 9

MATERIAL. Three fully-grown individuals ranging in diameter from 48 to 57 mm and two broken individuals with diameters of 24 and 28 mm. Sir Edward Belcher Collection.

DESCRIPTION. In the larger forms the surface is ornamented by 4–6 feebly-developed annuli which may form complete or incomplete rings. These sometimes fade into discrete granules (Figs 2b, 4b). The shell surface is otherwise smooth. The internal structure has been described by Carpenter who did not, however, mention the embryonic or nepionic chambers. A section of a juvenile microspheric individual in the Funafuti collection revealed four ana-nepionic chambers and 14 nepionic chambers following a proloculus with an internal diameter of approximately 20 µm. Hofker (1927) described a B form with a proloculus about 30 µm in diameter followed by a coil comprising 10 ana-nepionic and 14 nepionic chambers. Hanzawa (1951) reported a Recent B form (called *C. guembelianus*) with a proloculus diameter of 44 µm and a coil with one ana-nepionic and 15 nepionic chambers. He also described a Pleistocene form with a proloculus diameter of 40 µm, about three ana-nepionic and 18 nepionic chambers. These appear to be the only microspheric forms for which we have internal details. Chapman's (1900) B form from Funafuti was said to have a proloculus diameter of 140 µm but inspection of his illustration (pl. 3, fig. 2) shows that this measurement was incorrect.

Microspheric generation of *C. guembelianus*

Not known.

REMARKS. Cushman (1921) used *C. guembelianus* for all Recent cycloclypeids under the mistaken impression that Brady (1884) had referred the larger (microspheric) individuals in the Belcher collection to this species. But the sentence quoted by Cushman (1921 : 386) actually refers to *C. carpenteri*. Chapman (1900) thought that *C. guembelianus* merely comprised very young specimens of the A generation of *C. carpenteri*; he adduced no evidence for this although we believe that he was intuitively correct. Hofker (1927) 'preferred' to use the name *C. carpenteri* for all living cycloclypeids although he gave no clear reason, and Hanzawa (1951) used *C. guembelianus* for Recent specimens having 2–5 nepionic septa in the A1 and A2 generations regardless of the presence or absence of ornament.

CONCLUSIONS. It is clear from the present observations that *C. carpenteri* and *C. guembelianus* cannot be differentiated either by size or by ornament, and there remains only the possibility that their internal structures might be different. Table 1 compares the principal internal characters of the two 'species'. As the original megalospheric specimens of *C. carpenteri* appear to be abnormal in that they possess multi-embryonic chambers, they are not suitable for comparative purposes; Chapman's material from Funafuti is therefore used instead.

Table 1

Species	Proloculus diameter	Deuteroconch diameter	No. of ana-nepionic chambers	No. of nepionic chambers	No. of neanic ch. in 0·75 mm radius
C. guembelianus	190 µm	360 µm	1	2 or more	2 or 3
(syntypes)	200 µm	370 µm	1	2	5
C. carpenteri Funafuti (6 specimens)	150–230 µm	220–450 µm	1	1–6	2–5 (or ? 6)

It follows that only one living species of *Cycloclypeus* has been found and that this should be called *C. carpenteri*.

Failure to distinguish an ornate and an inornate living species poses a problem for palaeontologists since MacGillavry (1962), working on Oligocene assemblages from Spain, recognized an inornate lineage which he referred to *C. guembelianus* and an ornate lineage which he called *C. carpenteri*; Cosijn (1938) used a similar terminology. However, neither author studied Recent populations nor did they examine the type specimens of these species.

Subgenus *KATACYCLOCLYPEUS* Tan, 1932

TYPE SPECIES. *Cycloclypeus annulatus* Martin, 1880.

Tan erected *Katacycloclypeus* for cycloclypeids which possess one or more annuli in the megalospheric generation. As originally defined it included the following species: *C.* (*K.*) *annulatus* Martin (3 annuli), *C.* (*K.*) *biplicatus* Tan (2 annuli), *C.* (*K.*) *transiens* Tan (1 annulus and surface pustules) and *C.* (*K.*) *posttransiens* (1 annulus and no surface pustules). *C. martini* van der Vlerk (1923) should also have been included since it was described as having at least one annulus in the megalospheric form.

Unfortunately, the possession of a single annulus in the megalospheric generation is not absolutely diagnostic of *Katacycloclypeus* since certain species of *Cycloclypeus*, e.g. *C. posteidae* Tan, may, or may not, possess an annulus.

Tan believed that he could recognize an evolutionary sequence within *Katacycloclypeus* and planned to describe it in a later paper, which, unfortunately, never appeared. There is, however, sufficient information in his original publication (1932) for us to be able to deduce the main outline of his evolutionary scheme. He stated (1932 : 119) that the most primitive form of the subgenus was *C.* (*K.*) *transiens* and that this evolved from *C.* (*C.*) *eidae*. From his table V it is apparent that his first record of *Katacycloclypeus* (*K.* sp.) was from beds a little younger than those yielding good Te$_5$ (= Aquitanian) assemblages including *Eulepidina*, *Spiroclypeus* and *C. eidae*. *C.* (*K.*) *biplicatus* was reported from slightly younger strata along with 'very seldom' specimens of *C. annulatus*, the latter becoming progressively more numerous until it dominated the katacycloclypeid fauna of supposed Late Vindobonian age. All the strata in which Tan found *Katacycloclypeus* can now be assigned to Tertiary lower *f*, and we may, therefore, conclude that Tan's evolutionary sequence was intended to be *C. eidae* → *C.* (*K.*) *transiens/posttransiens* (6–13 heterosteginoid chambers) → *C.* (*K.*) *biplicatus* (unknown number of heterosteginoid chambers) → *C.* (*K.*) *annulatus* (*c.* 3 heterosteginoid chambers in the types; 2–4 in our additional material from Java). It is evident that forms referable to *C.* (*K.*) *annulatus* appeared fairly early in the sequence and came to dominate the faunas later. We may reasonably infer that *C.* (*K.*) *posttransiens* followed *C.* (*K.*) *transiens* in the evolutionary sequence but whether it occurred together with *C.* (*K.*) *biplicatus* is uncertain.

Van der Vlerk (1923) described *C. martini* from strata that are clearly of Tertiary lower *f* age since they contain *Flosculinella bontangensis* (Rutten). He illustrated four specimens, one of which (pl. 2, fig. 4) he regarded as microspheric, although in the light of later knowledge it is seen to be a megalospheric individual with a rather small proloculus (internal diameter 0·37 mm) and about six heterosteginoid chambers. His diagnosis must therefore be amended to include forms with one to six nepionic chambers, in which case it embraces *C.* (*K.*) *annulatus*. However, the latter is supposed to possess three annuli whereas van der Vlerk's species has only one or two. A small piece of the type sample for *C. annulatus*, provided by the Rijksmuseum Leiden, has enabled us to section three broken megalospheric specimens and to show that they possess one ana-nepionic and two to four nepionic chambers (Figs 19, 20).

It is apparent that without a better knowledge of the internal structure and morphological variation of the seven species and varieties of *Katacycloclypeus* so far described, it is impossible to distinguish between them. Since *C.* (*K.*) *annulatus* appears at an early stage in the evolutionary history of the subgenus it seems unlikely that the number of annuli is a feature of major taxonomic significance. This being so, it is proper, for the time being at least, to regard *Katacycloclypeus* as a single evolving monotypic lineage largely confined to the Middle Miocene, and which, in a period of about 4 Ma, reduced the number of nepionic chambers in the megalospheric coil from 6 to 13 (in the most primitive forms) to 0–2 in the most highly evolved forms found in Fiji (see below).

Cole (1975) advocated the abandonment of the subgeneric name *Katacycloclypeus* on three grounds: (1) that the annular inflations were probably ecologically produced growth phenomena, (2) that individuals belonging to the same species could sometimes be assigned to different subgenera and (3) that the use of this subgeneric name could induce a false confidence that any annulate specimens were necessarily of T*f* age. He did not, however, demonstrate that the annuli represent resting stages in growth, and the fact that they are well developed only in certain Miocene species suggests that they are not. Furthermore, the irregular development of annuli in microspheric forms, and in particular the tendency for individual annuli to fade out over part of the test, is inconsistent with the resting stage hypothesis. Whether or not *Katacycloclypeus* is confined to the T*f* stage is irrelevant to the biological validity of the name. Only the fact that individuals of the same species can sometimes be assigned to two subgenera is of substantive importance, and Tan was aware of this when he erected *Katacycloclypeus*. We believe that it will be necessary to examine assemblages rather than isolated individuals in order to determine whether or not this objection is valid, and as yet this has not been done.

Cycloclypeus* (*Katacycloclypeus*) *annulatus Martin, 1880
Figs 12–15, 17–23

1880 *Cycloclypeus annulatus* Martin : 157; pl. 28, fig. 1.
1923 *Cycloclypeus martini* van der Vlerk : 138; pl. 1, figs 1, 2; pl. 2, figs 3, 4.
1932 *Cycloclypeus* (*Katacycloclypeus*) *annulatus* Martin; Tan : 39.
1932 *Cycloclypeus* (*K.*) *annulatus* Martin; Caudri : 190; pl. 1, figs 1–3.
Not 1934 *Cycloclypeus annulatus* Martin; Whipple : 142; pl. 19, fig. 1.
1945 *Cycloclypeus* (*K.*) *annulatus* Martin; Cole : 282; pls 19A, 20G (not H).

The types of *C. annulatus* came from 'Die Kluft des Tji Tarum bei Tjikao, nördlich vom Gunung Parang, West Java'. A small fragment of Martin's original material from the Rijksmuseum Leiden has enabled us to prepare several additional thin sections including three orientated in the equatorial plane (Figs 15, 19, 20). The following descriptions are based on topotypes.

Megalospheric generation
Figs 15, 19, 20

Description. Test moderately large, ranging in diameter from 4 to 7 mm. Surface ornamented by at least two strongly inflated annuli. Signs of surface granulation visible externally on some specimens but not on others, although thin sections show that pillars are always present in the annuli and over the central part of the test. Embryonic apparatus large. Proloculus subovate, thin-walled, and partly embraced by the larger, thicker-walled, reniform second chamber. One ana-nepionic chamber (divided by a single septum in one specimen) is followed by 2–4 nepionic chambers. Early neanic chamberlets shorter (radially) than wide, but lengthening after the third chamber until radially elongate chambers are dominant after the 5th to 7th annular chamber. Stolon system distinct; canal system not seen.

Dimensions (based on 3 specimens).

Proloculus	228 μm (min)	to	335 μm (max)
Deuteroconch	350 μm (min)	to	480 μm (max)

Remarks. As this material is relatively poorly preserved and shows signs of abrasion and breakage, it is possible that well-preserved specimens would show surface pustules and might possess more than two annuli. These specimens differ from the types in that the second chamber less strongly envelops the proloculus. However, as the types of *C.* (*K.*) *martini* v.d. Vlerk (1923 : pl. 1, fig. 2; pl. 2, figs 3, 4) also show considerable differences, this character is obviously highly variable and requires statistical investigation.

Megalospheric forms from Fiji
Figs 14, 17, 18, 22, 23

MATERIAL. Numerous specimens from samples F 172, F 173b, F 175 and F 181 (Ladd's layers 8, 7, 5 and just below 1 respectively; see Ladd & Hoffmeister 1945 : 36), collected in stratigraphical order through the type section of the Futuna Limestone, Vanua Mbalavu, Fiji. Brown, iron-stained specimens occur in all four samples; white (unstained) individuals in F 132 and F 181. Most specimens somewhat abraded peripherally and therefore smaller than during life.

DESCRIPTION. Test moderately large (4–6 mm in diameter) with one or two prominent annuli; the broad central boss is unornamented, as is the rest of the test including the annuli. Embryonic apparatus very large, the ovate proloculus being strongly embraced by the reniform second chamber. Both chambers are thin-walled. Ana-nepionic chambers absent; nepionic chambers reduced to two or less. When the nepionic chambers are absent (Figs 18, 23), the embryonic apparatus is followed immediately by annular chambers. Early neanic chambers about twice as wide as long near the embryonic apparatus, but after the 4th to 6th chamber becoming slightly longer than wide. Canal system comprises a wide canal in each secondary septum which divides before reaching the primary septa thus producing two parallel smaller canals in the primary septum. Stolon system not observed in any of the sections studied.

DIMENSIONS (based on 10 thin sections).

Proloculus diameter	0·30 mm – 0·80 mm (usually 0·63 mm)
Second chamber	0.59 mm – 1·25 mm (usually 0·90 mm)
Thickness of prolocular wall	10 μm – 20 μm (4 specimens)
Thickness of deuteroconch wall	10 μm – 40 μm (4 specimens)

The smooth external surface and numerous annuli distinguish the megalospheric generation from those of *C. eidae* and *C. posteidae* which are heavily ornamented and much smaller (Tan 1932). Stolon system not visible in the material studied; canal system as in *C. carpenteri*.

Microspheric forms from Fiji
Figs 12, 13, 21

DESCRIPTION (based on 9 specimens from the type section of the Futuna Limestone). Test thin, up to 90 mm in diameter. Small but distinct umbo surrounded by concentric annuli (usually 6–7 in a radius of 20 mm) which are often coarsely pustulate, particularly in the larger specimens. Annuli often incomplete towards the periphery of the test: remainder of shell surface smooth.

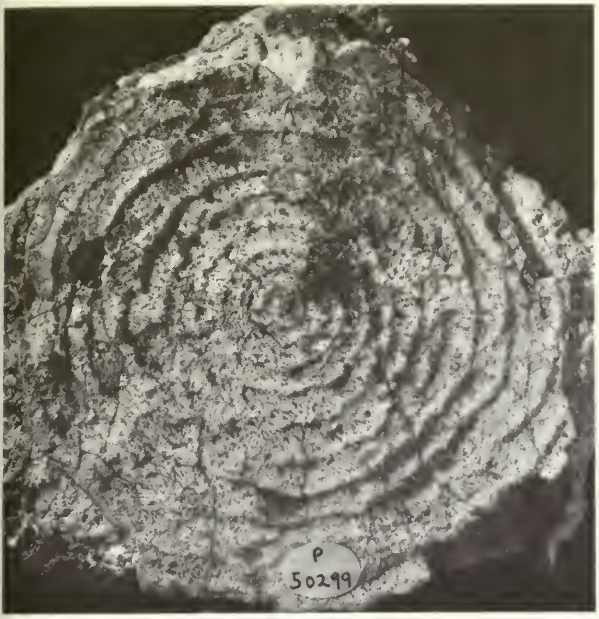
Figs 12, 13. *Cycloclypeus* (*Katacycloclypeus*) *annulatus* Martin, ×1. Microspheric individuals from samples F 180 and F 177, type section, Futuna Limestone, Vanua Mbalavu, Fiji. Note presence of numerous well-developed annuli in both specimens. These tend to be replaced by discrete granules and to fade out towards the periphery in some specimens (see Fig. 13). P.50299 and P.50298.

Fig. 14. *C.* (*K.*) *annulatus* Martin, ×5. Typical broken megalospheric form from Sample F 173b, Vanua Mbalavu, Fiji (cf. Fig. 16). Better-preserved specimens show at least two annuli. Specimen sectioned and registered as P.50466.

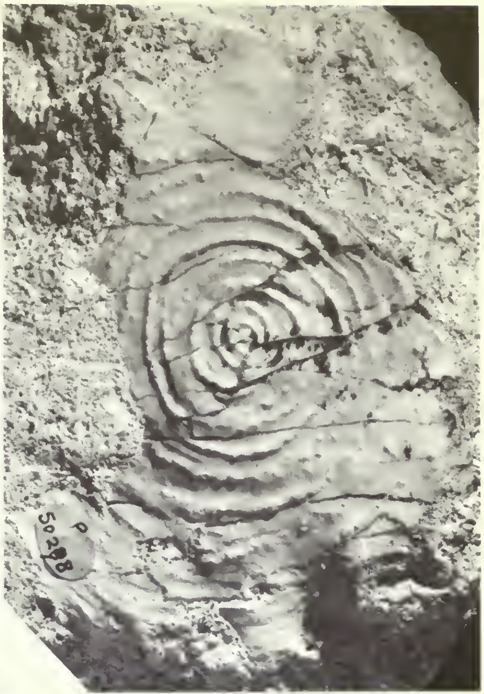
Fig. 15. *C.* (*K.*) *annulatus* Martin, c. ×35. Thin section showing the embryonic apparatus and nepionic stage. Topotype from Java. Ex Martin Collection, Leiden. Note undivided ana-nepionic and 4–6 nepionic chambers. P.50464. Test damaged and repaired during life.

Fig. 16. *C.* (*C.*) *posteidae* Tan, ×10. Sample F 181, Futuna Limestone, Vanua Mbalavu, Fiji. Introduced to illustrate that the megalospheric form of *C. posteidae* can closely resemble *C.* (*K.*) *annulatus* externally although they are quite different internally. Compare with Fig. 14; see also Fig. 1a.

Figs 17, 18. *C.* (*K.*) *annulatus* Martin, ×21 and ×20. Thin sections of megalospheric individuals from sample F 181, Futuna Limestone, Vanua Mbalavu, Fiji. Neither specimen possesses an ana-nepionic chamber; Fig. 17 (P.50462) shows two nepionic chambers and Fig. 18 (P.50463) no nepionic chambers. See also Figs 22, 23.



12



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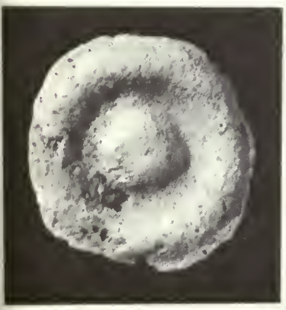

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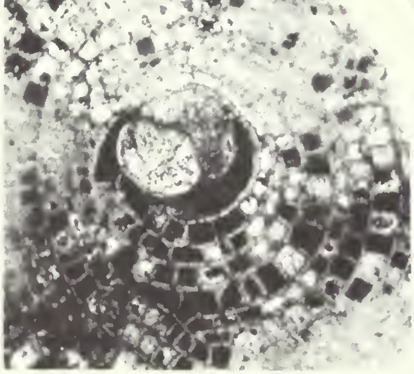

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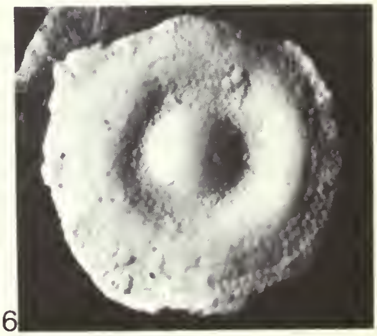

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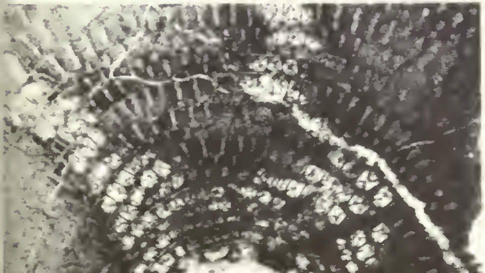

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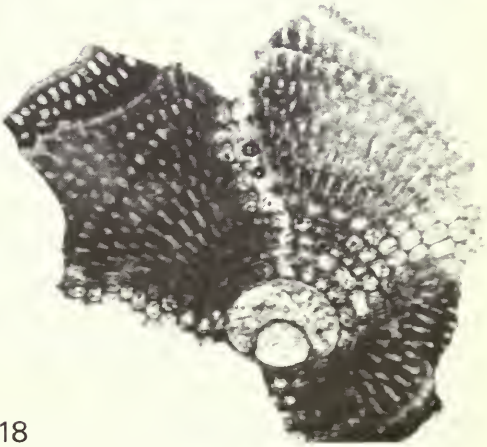

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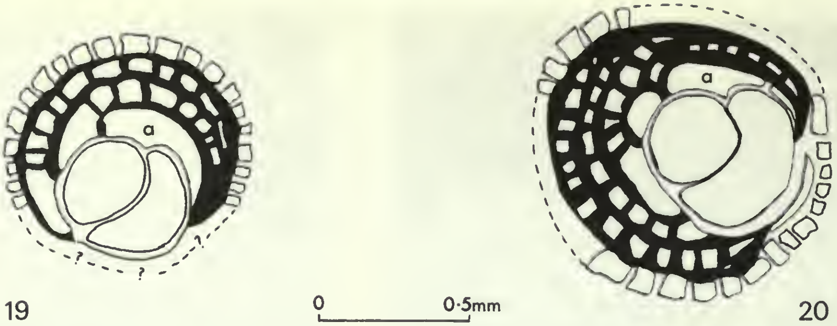


19

20

Fig. 19, 20. Internal structure of two topotype specimens of *C.* (*Katacycloclypeus*) *annulatus* Martin. Part of Martin's original material from Java. The first specimen (Fig. 19) shows at least three nepionic chambers including one undivided ana-nepionic chamber. Fig. 20 shows five nepionic chambers. The ana-nepionic chamber is divided by a single septum in this specimen. Fig 19, P.50464; Fig. 20, P.50465.

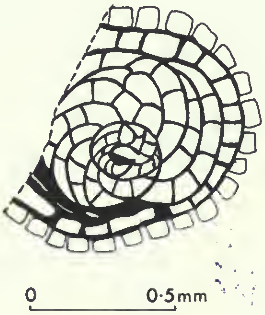
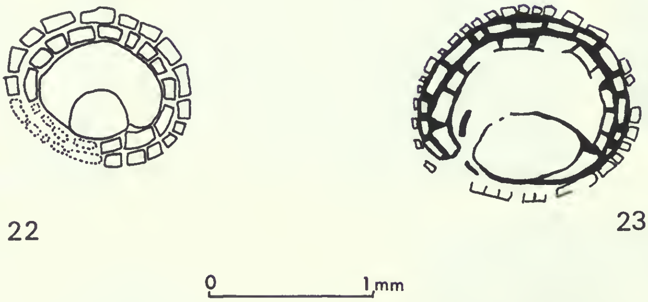


Fig. 21. *C.* (*K.*) *annulatus* Martin. Microspheric form from the Futuna Limestone, Fiji. The section just misses the proloculus but clearly shows that there are at least six undivided (operculinoid) chambers and about 15 divided (heterosteginoid) chambers in the nepionic stage. P.50298.



22

23

Figs 22, 23. *C.* (*K.*) *annulatus* Martin. Embryonic apparatus of megalospheric individuals from the Futuna Limestone, Fiji, illustrated in Figs 17, 18. Note absence of nepionic chambers in Figs 18, 22. Figs 17, 23, P.50462; Figs 18, 22, P.50463.

The small proloculus and second chamber are followed by a coil comprising at least 8 ana-nepionic chambers and about 16 nepionic chambers. The first nepionic chamber is divided by a single septum. Early neanic chamberlets slightly shorter than wide but becoming longer than wide after the 7th or 8th chamber: towards the margin they are very elongate (2–3 times longer than wide). Stolon system not observed. The primary septa contain two canals, the secondary septa only one.

Remarks. The cycloclypeids from the Futuna Limestone of Fiji are the largest calcareous foraminifera known. Our specimens (up to 90 mm in diameter) are considerably larger than the types of *C.* (*K.*) *annulatus* from Java, and even bigger individuals have been observed in the field: Cole (1945) measured specimens up to 100 mm in diameter from the type section, while Ladd & Hoffmeister (1945 : 36) mentioned specimens of up to 6 inches (=152 mm) in diameter. The embryonic apparatus in the megalospheric form is also much larger than in the types of *C.* (*K.*) *annulatus* while the reduction of the ana-nepionic and nepionic chambers provides a further striking difference. However, these characters could merely reflect the fact that the proloculus itself is so much larger, in which case they are not of fundamental importance. Proloculus size is, however, a very poor taxonomic character in foraminifera and should be used only with caution.

The most important feature of the Futuna Limestone specimens is that some of them have reduced the nepionic spire completely. No further evolution of this character is possible, and it may be significant that having reached this stage, the species (and subgenus) became extinct.

ASSOCIATED FAUNA. *Cycloclypeus* (*C.*) *posteidae hexasepta* Tan, *C.* cf. *C.* (*C.*) *posteidae dodekaseptus* Tan and *C.* cf. *C.* (*C.*) *eidae heneikaseptus* Tan; the last two are remarkable in that they possess very small proluculi – smaller than those of the microspheric generations as described by Tan – and yet in all other characters closely resemble the megalospheric forms. *Lepidocyclina rutteni* van der Vlerk and *L. martini* (Schlumberger) are also present.

Planktonic foraminifera include more than 25 species, but the association of *Globigerina nepenthes* Todd *picassiana* Perconig, *Globigerinoides bollii* Blow, *Gs. subquadratus* Brönnimann, *Gs. parkerae* Bermudez, *Globigerinita glutinata* (Egger), *Gt. glutinata juvenalis* (Bolli), *Globorotalia* (*Turborotalia*) *siakensis* (LeRoy), *Gr.* (*T.*) *continuosa* Blow and *Gr.* (*Gr.*) *cultrata* (d'Orbigny) *limbata* (Fornasini) establishes the age as N13/14 (probably N14) in terms of Blow's (1969) zonation. The reduction of the nepionic coil to 0–2 chambers in *C.* (*K.*) *annulatus* supports this late Middle Miocene age.

Evolution

Tan (1932), in an elaborate and rather difficult paper, described an evolutionary series in *Cycloclypeus* beginning with *C. koolhoveni* Tan (21–38 nepionic chambers in the A form) in the Oligocene and ending with the Recent *C. carpenteri* (1–6 nepionic chambers: this paper). His numerous subspecies have not stood the test of time, most specialists preferring to recognize five or six main species. However, Cosijn (1938) and MacGillavry (1962) concluded that *C. carpenteri* evolved directly from *C. eidae* in the Miocene, thus eliminating the need to recognize *C. posteidae* and the *C. indopacificus* Tan group. They did not, however, study the living representatives of the genus on which this species is based, but assumed that the presence of a short nepionic coil in a few Miocene specimens proved their point. Notwithstanding this, all authors are agreed that the early Oligocene cycloclypeids had a long initial coil comprising some 21–38 chambers in the megalospheric form, and that this was eventually reduced to 2 or 3 nepionic chambers, a process known as nepionic acceleration. The greater part of this shortening had already taken place by Middle Miocene times.

The subgenus *Katacycloclypeus* has been little studied since 1932, presumably because authors thought of it as comprising a different evolutionary lineage, the presence of annuli having been regarded (for no very good reason) as a character of fundamental taxonomic importance. If reduction of the ana-nepionic and nepionic chambers in *Cycloclypeus* is accepted as an indication of the grade of evolution, then *C.* (*K.*) *annulatus* s.l. is not only the largest, but also the most highly evolved member of the genus, notwithstanding the fact that it is extinct and that more 'primitive' members live on today. If the history of this subgenus has any predictive value, *C. carpenteri* must now be on the verge of extinction and will disappear when it loses its initial coil.

We believe that Tan (1932) and MacGillavry (1962) were justified in regarding species of *Katacycloclypeus* as representing a separate lineage from those species of *Cycloclypeus* which led eventually to *C. carpenteri*.

Drooger (1955) studied numerous specimens of *Cycloclypeus* s.s. from samples of early *f* age from Borneo, and concluded that the number of nepionic chambers depended on two factors, nepionic acceleration and the size of the proloculus. He thought that the former acted to reduce the number of heterosteginoid chambers, and the latter to decrease the number of operculinoid chambers in the microspheric generation, and, above a certain size, the number of heterosteginoid chambers in both generations.

Conclusions

The foregoing evidence permits us to draw the following conclusions.

1. The range of the genus *Cycloclypeus* is Early or Middle Oligocene to Recent, *C. mammillatus* Carter having been shown to be from strata of Late Oligocene age and not from the Eocene as originally stated.

2. *C. carpenteri* Brady is a subjective senior synonym of *C. guembelianus* Brady, and there is no evidence to suggest that more than one species is alive today.

3. *C. carpenteri* should be declared the type species of *Cycloclypeus*, and *C. mammillatus* Carter, which was described from a single unfigured specimen, should be allowed to fall into disuse.

4. It is not possible to recognize more than one species of *Katacycloclypeus* at present. So far as can be ascertained, neither surface ornament nor number of annuli are of great taxonomic significance, and it will not be possible to use the embryonic apparatus and nepionic coil satisfactorily until an adequate number of specimens from well-dated horizons throughout its complete range have been collected and investigated statistically. It might then be possible to recognize a primitive group with some 6–13 nepionic chambers (perhaps *C.* (*K.*) *transiens*), an intermediate group with 2–5 nepionic chambers (*C.* (*K.*) *annulatus*) and an advanced group with 0–2 nepionic chambers (*C.* (*K.*) *martini*). This cannot, however, be done at present and it is therefore best to refer them all to *C.* (*K.*) *annulatus*.

5. It is currently convenient to regard *Katacycloclypeus* as a subgenus of *Cycloclypeus*, but for biostratigraphical rather than biological reasons. It is not possible to state that the mere possession of annuli is a character of diagnostic importance at generic level although it has some significance at species level, at least in the megalospheric form.

6. All published references to *Katacycloclypeus* from strata which are not clearly of Tertiary e_5 or f_{1-2} age should be treated with caution. The subgenus can be recognized only from properly orientated thin sections or from matrix-free megalospheric individuals. In random thin sections of limestone it can easily be confused with *Cycloclypeus* (*Cycloclypeus*).

7. The presence or absence of surface ornament (granules or pustules) can only be regarded as significant after vertical sections have been examined, since secondary (organic) calcification often obscures the primary ornament.

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The provenance of *Sivapithecus africanus*

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Synopsis

Controversy over the taxonomic affinities of *Sivapithecus africanus* from Miocene deposits in Kenya has been increased by doubts about its provenance. One specimen is known to be from middle Miocene deposits on Maboko Island, and the only other specimen of 'known' provenance is the type specimen (M 16649), which is reported as coming from Rusinga Island. There is considerable doubt over this, however, so X-ray fluorescence spectrometry (XRF) of the matrix of M 16649 has been attempted to try and establish its site of origin. The XRF spectrum for M 16649 shows great differences from the range of patterns found for the Rusinga Island sites, and it shows the greatest similarity with the spectra from several different levels of the Maboko Island deposits. In some ways, however, the XRF spectrum for M 16649 is unlike any of the samples tested, so while it can be concluded that this specimen probably did not come from Rusinga Island, it is not yet clear where it did come from.

Introduction

Sivapithecus africanus was first described in 1950 on the basis of a maxilla (registration number M 16649) and two isolated teeth (Clark & Leakey 1950, 1951). These specimens differ morphologically from other East African Miocene dryopithecines, although the maxilla was initially assigned (MacInnes 1943) to a species of *Proconsul* Hopwood 1933. Clark & Leakey (1950, 1951), in the first major revision of the East African Miocene Hominoidea, redescribed the specimens and recognized their differences from other specimens of *Proconsul* by assigning them to a new species of the Asian middle to late Miocene genus *Sivapithecus*. This view gained some measure of support when Simons & Pilbeam (1965) synonymized *S. africanus* with a previously-described species of the same genus, calling it *Dryopithecus* (*Sivapithecus*) *sivalensis* (Lydekker, 1879). Two years later, Leakey (1967, 1968), who never accepted Simons & Pilbeam's synthesis, referred *Sivapithecus africanus* to the genus *Kenyapithecus*, which had as its type species *K. wickeri* from Fort Ternan, Kenya (Leakey 1962). Pilbeam (1969) and Andrews (1971, 1973) later synonymized *Kenyapithecus* with *Ramapithecus* and referred all the '*K. africanus*' specimens, including M 16649, to species of *Proconsul* (or as it then was, *Dryopithecus*). The situation still remains, however, that these specimens are very distinctive, with at least two autapomorphic characters and only one synapomorphy with later Miocene species of *Ramapithecus*, *Sivapithecus* and *Dryopithecus*, so that on present evidence there is no justification for retaining them either in *Proconsul* or in *Sivapithecus*. This uncertainty is increased by doubts over the provenance of two of the three known specimens.

One of the isolated teeth attributed to '*Sivapithecus africanus*' is the only specimen of confirmed provenance. This is an upper molar (specimen CMH 26 in Clark & Leakey 1951; KNM-MB 107 in Andrews 1973) and it is said to be from middle Miocene deposits on Maboko Island, Kenya. The other isolated tooth is from an unknown locality in western Kenya (Clark & Leakey 1951), and the third and only other specimen is the type specimen, M 16649, which is said by Clark & Leakey (1951) to have been recovered from early Miocene deposits at R106 on Rusinga Island, Kenya. In the first description of the specimen, however, MacInnes (1943) did not identify the locality: the collection as a whole was made in 1932–35 by L. S. B. Leakey's East African Archaeological Expeditions to Rusinga Island and Songhor, but at least one of the specimens, the mandible of a cercopithecoid primate, is almost certainly not from these early Miocene deposits but from Maboko Island, three to four million years later in time. Because the preservation of M 16649 is unlike that of other specimens known to be from Rusinga Island, and in particular R106, we

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Table 1

Tube anode	current	voltage	crystal	detector	path	window	attenuation
Tungsten	30 MA	60 kV	LiF 200	flow counter	air	1·0–∞	2^2
Chromium	30 MA	60 kV	LiF 200	flow counter	air	1·0–∞	2^2

Table 2

2θ scanning speed	chart speed	full scale deflection	time constant
2°/min. betw. 15° and 126°	25 mm/min.	1000 counts/sec.	0·4 or 1·0 sec.

Notes on Table 3

Zirconium (Zr) $K\alpha_{1,2}$ (22·55°), $K\beta_1$ (20·07°), $K\alpha_{1,2}$ (2nd order 46·04°), $K\alpha_{1,2}$ (4th order 102·91°). It is difficult to assess the presence of zirconium by XRF since at most angles the line is masked by strontium, which is usually the more abundant element. By checking for other lines, e.g. $K\beta_1$ (20·07°), and by comparing the strontium $K\alpha_{1,2}$ (25·15°) line with the zirconium $K\alpha_{1,2}$ (22·55°) plus strontium $K\beta_1$ (22·42°) line, it was possible to deduce the presence or absence of zirconium in the sample. Zirconium was present in 10 of the 14 samples from Rusinga but in only 4 of the 7 samples from Maboko and 1 of 4 samples from Songhor. There was no indication of the presence of zirconium in the *Sivapithecus* sample.

Yttrium (Y) $K\alpha_{1,2}$ (23·80°). Yttrium is clearly present in the *Sivapithecus* matrix and in most of the samples from Maboko and Songhor (6 out of 7 and 3 out of 4 samples respectively). On the whole it is not an important element in the samples from Rusinga although it is clearly present in M 15323 from R106.

Rubidium (Rb) $K\alpha_{1,2}$ (26·62°). Rubidium is a more important constituent of most of the Rusinga samples than it is of the Maboko ones. It was not detected in the *Sivapithecus* matrix.

Lead (Pb) $L\alpha_1$ (33·93°), $L\beta_1$ (28·26°). Lead $L\alpha_1$ and $L\beta_1$ lines were observed in the matrix of *Sivapithecus*. They were most clearly present again in the matrix of M 16632 from Maboko. Small $L\alpha_1$ peaks were seen in the spectra for several other samples from Maboko. Only two or possibly three samples from Rusinga had a very small quantity of lead.

Zinc (Zn) $K\alpha_{1,2}$ (41·80°), $K\alpha_{1,2}$ (2nd order 91·04°). Zinc was present in all the samples, but the lines were particularly strong in the *Sivapithecus* spectrum and in the spectra for M 16632 (Maboko) and M 32949 (Mfwangano).

Copper (Cu) $K\alpha_{1,2}$ (41·80). Copper is not an important constituent of the *Sivapithecus* matrix nor of the samples from Maboko. In every case it was more important in the samples from Rusinga and Songhor. This was clearly further demonstrated in the chromium tube spectra.

Nickel (Ni) $K\alpha_{1,2}$ (48·67). A similar picture was noted for nickel.

Neodymium (Nd) $L\alpha_1$ (72·13°). Neodymium, if correctly identified, is present in the *Sivapithecus* sample and in 4 out of 7 of the Maboko samples but in only 3 out of 14 of the samples from Rusinga. It was not detected in the samples from Songhor.

Vanadium (V) $K\alpha_{1,2}$ (76·94°). The vanadium $K\alpha_{1,2}$ line at 76·94° tends to be difficult to distinguish from the titanium $K\beta_{1,3}$ line at 77·27°, but it is clearly present in the spectrum of the *Sivapithecus* matrix (where the titanium content is low) and of all except one of the samples from Maboko. Vanadium was detected in only one of the Rusinga samples (M 32847).

Titanium (Ti) $K\alpha_{1,2}$ (86·14°). Titanium is a minor constituent in the *Sivapithecus* matrix and in most of the samples from Maboko and Songhor whereas it is an important element in at least half of the samples from Rusinga.

Barium (Ba) $L\alpha_1$ (87·17°). Barium was clearly present in the *Sivapithecus* matrix and in all except one sample from Maboko, but was detected in only a few samples from Rusinga, when it was observed at low levels.

Table 3 XRF readings expressed as a proportion of the tungsten (W) $L\gamma_1$ line $2\theta = 31{\cdot}66°$

Locality	Specimen number	Nb $K\alpha_{1,2}$ 21·40	Zr $K\alpha_{1,2}$ 22·25	Y $K\alpha_{1,2}$ 23·80	Sr $K\alpha_{1,2}$ 25·15	Rb $K\alpha_{1,2}$ 26·62	Pb $L\alpha_1$ 33·93	Zn $K\alpha_{1,2}$ 41·80	Cu $K\alpha_{1,2}$ 45·03	Ni $K\alpha_{1,2}$ 48·67	Cr $K\alpha_{1,2}$ 69·36	Ce $L\beta_1$ 71·06	Nd $L\alpha_1$ 72·13	V $K\alpha_{1,2}$ 76·94	Ti $K\alpha_{1,2}$ 86·14	Ba $L\alpha_1$ 87·17	K $K\beta_{1,3}$ 118·30
(Mylar only)	blank	0	0	0	0	0	0	4·0	10·0	3·0	0	0	0	0	0	0	0
?	*Sivapithecus africanus* M 16649	3·0	nd	6·0	53·0	nd	12·0	45·0	20·0	10·0	4·0	5·0	3·0	pres	23·0	10·0	3·0
Rusinga																	
R1	M 21341	1·6	nd	2·4	56·0	2·6	2·6	24·8	24·8	10·5	2·4	2·4	nd	nd	44·6	nd	4·8
R2	M 32834	4·4	pres	nd	46·6	4·4	nd	27·3	59·0	13·2	6·2	nd	nd	nd	74·8	nd	3·5
R3	M 32447	nd	nd	nd	25·6	nd	nd	10·5	23·5	11·5	2·4	nd	nd	nd	44·9	3·2	0·8
R7	M 25168	nd	nd	nd	62·1	nd	nd	6·8	21·3	11·9	2·6	nd	nd	nd	23·8	nd	0·9
R7	M 32838	2·0	pres	1·0	31·0	nd	nd	11·0	26·0	9·0	2·0	2·0	2·0	nd	40·0	1·0	nd
R74	M 34115	2·3	pres	nd	18·2	2·3	1·5	11·4	19·8	10·6	3·0	nd	nd	nd	58·5	5·3	0·8
R105	M 18920	2·2	pres	nd	26·2	3·3	nd	19·8	25·2	12·1	5·5	2·2	1·1	nd	88·0	nd	5·5
R105	—	1·6	pres	2·4	40·3	3·2	nd	23·7	28·4	10·3	2·4	2·4	nd	nd	71·1	nd	4·0
R106	M 15320	1·5	pres	0·8	39·5	2·3	nd	16·7	23·6	7·6	2·3	nd	nd	nd	50·2	nd	3·0
R106	M 15323	1·8	pres	5·3	74·8	1·8	nd	16·7	30·8	7·9	5·3	7·0	4·4	nd	46·6	nd	2·6
R106	M 32363	2·3	pres	nd	32·4	2·3	nd	21·1	27·5	16·2	4·9	nd	nd	nd	60·8	nd	2·4
R106	M 32847	1·7	pres	nd	29·8	1·7	nd	11·1	26·4	10·2	3·4	nd	nd	nd	57·8	1·7	0·9
R106	—	nd	nd	1·1	75·9	1·1	nd	14·1	25·2	11·1	4·4	6·6	nd	nd	38·5	nd	2·2
R107	M 25270	3·1	pres	1·6	26·8	2·4	?	24·5	33·2	10·3	8·7	1·6	nd	nd	71·1	nd	2·4
Maboko																	
	M 15310	3·4	pres	2·6	25·5	?	nd	18·7	16·2	9·4	8·5	1·7	nd	nd	68·0	4·3	0·85
	M 15438	2·4	nd	3·2	57·7	0·8	1·6	12·6	11·9	5·5	2·4	nd	1·6	pres	34·0	3·2	2·4
primate level	M 16331	2·3	pres	2·4	64·8	0·8	1·6	15·4	20·3	7·3	3·2	nd	1·6	pres	45·5	16·2	2·4
primate level	M 16332	2·9	pres	3·8	73·0	nd	4·8	39·4	19·2	5·8	1·9	3·8	2·9	pres	17·3	3·8	1·0
	M 30085	4·0	nd	2·0	45·0	2·0	nd	13·0	nd	6·0	nd	nd	nd	pres	11·0	nd	1·0
	M 32748	2·8	nd	nd	54·3	nd	1·8	17·5	21·2	7·2	3·7	1·0	0·9	pres	78·2	16·6	?
		3·3	pres	1·6	38·9	1·6	3·2	16·2	12·2	7·3	4·1	nd	nd	pres	47·8	4·1	nd
Songhor																	
	M 32730	0·8	pres	1·6	34·0	nd	2·4	25·9	17·0	6·5	3·2	2·4	nd	pres	21·1	4·9	?
	M 34117	nd	nd	nd	11·4	1·8	nd	15·8	30·8	11·4	7·9	nd	nd	nd	66·0	2·6	?
Bed 9	Sgr 1	5·8	nd	1·2	27·8	?	nd	32·5	31·3	16·2	8·1	?	nd	nd	30·2	nd	nd
Bed 5	Sgr 2	3·7	pres	1·5	33·6	2·2	1·5	21·2	20·4	13·1	7·3	2·9	nd	pres	28·5	nd	1·5
Other sites																	
Arongo Uyoma	—	3·2	nd	1·6	47·0	2·4	nd	8·9	19·4	8·9	1·6	0·8	nd	pres	34·0	1·6	0·8
Mfwangano	M 32949	9·3	nd	1·7	63·8	2·6	2·6	41·7	16·2	6·8	1·7	3·4	2·6	pres	17·0	2·6	0·9
Ombo	M 29427	nd	nd	nd	67·2	1·7	3·4	17·0	25·5	17·0	3·4	0·9	nd	pres	23·8	1·7	nd

have examined the matrix from the specimen by qualitative X-ray fluorescence analysis and compared it with matrix samples from a number of Miocene localities in Kenya to try and determine which locality it may be from.

Methods and results

Matrices taken from 28 East African specimens in the collection of the British Museum (Natural History) were sampled. These represented six East African Miocene sites. We concentrated on material from Rusinga (14 samples), Songhor (4 samples) and Maboko (7 samples) and took single samples from several other sites.

X-ray fluorescence spectra were recorded using a Philips PW 1140 generator, PW 1540 goniometer and PM 800 flat bed recorder. Samples of the finely powdered matrix of 150–160 mg were weighed out and distributed in an even layer over a Mylar film in a standard Philips sample holder before being placed in the X-ray beam. Instrument and running parameters are listed in Tables 1 and 2. A blank Mylar film was run to determine impurities in the tube.

Eight of the samples, including the matrix of M 16649, were run again in the same conditions but using larger samples of powder (500–700 mg) and a chromium tube in place of the tungsten tube. This allowed a check to be made for those elements (tungsten, nickel, vanadium) that are masked by the lines of the tungsten X-ray tube. The spectra derived from the different tubes, however, cannot be compared directly since some elements are energized more readily by one tube than by the other.

A rough estimate of the relative abundance of the different elements present was made by measuring the heights of the lines presented by each sample. These heights were all normalized to the tungsten $L\gamma_1$ line at $2\theta = 31 \cdot 66°$. The figures obtained, while not calibrated for quantitative determination, were tabulated (Table 3) so that comparisons can be made of the different samples with each other and with the sample from M 16649. The plot for M 16649 was read last to avoid bias in interpretation.

Conclusions

RUSINGA ISLAND. In general the matrix samples from Rusinga Island have relatively high concentrations of copper, iron and titanium and contain appreciable amounts of zirconium. Zinc and manganese are not important constituents. Yttrium and barium are often not present and it is unusual for the material to contain lead or vanadium. Rubidium is usually present.

MABOKO. The samples from Maboko contain relatively high levels of manganese and vanadium. Zinc, copper, iron, titanium and potassium are less important than they are in samples from Rusinga. Yttrium, lead and barium are usually present whereas rubidium is only present in very minor quantities.

SONGHOR. The four samples from Songhor have relatively low concentrations of zirconium, lead, zinc, iron or vanadium. Strontium, titanium and calcium can also be rather low. Neodymium was not detected in any of the four samples nor was potassium clearly present in three of them.

Sivapithecus africanus, M 16649. The matrix from this specimen contained relatively high levels of zinc, manganese, vanadium and calcium, but comparatively low levels of copper, iron and potassium. There were clear peaks for yttrium, lead, neodymium and barium. Rubidium was not detected and zirconium is probably not present. The presence of yttrium, barium, neodymium, lead and vanadium and the absence of rubidium make up a pattern that is very different from the Rusinga pattern. In many respects the XRF spectrum of M 16649 is more like those from the Maboko Island samples, but between these also there are differences, for instance in the presence of rubidium and lower levels of lead in the Maboko samples. It is concluded, therefore, that there are very strong reasons for doubting the reports that M 16649 is from R106 on Rusinga Island and that it may be from Maboko Island, but that the data are insufficiently conclusive to show definitely which site it may be from.

The results of this analysis would seem to indicate the value of carrying out further work along these lines. In the first instance, samples of controlled provenance should be collected rather than relying on matrix samples from specimens collected many years ago. A wider variety of localities could be sampled and much larger samples would be available, and in addition to XRF their mineralogical and elemental characteristics could be determined.

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Postscript

Since writing this report, Dr Martin Pickford has found in the collections of the British Museum (Natural History) the broken fragment of a left P_3 from Maboko Island. It is clearly labelled as coming from Maboko Island and has been registered M 36370. It has the same combination of grey enamel and white bone seen on M 16649 and, although no matrix is preserved so that it cannot be compared directly with that specimen, the colour similarity, which is unique to these two specimens from the Miocene of East Africa, must be considered additional indication that they both originated from Maboko Island. The specimen itself has a robust crown with a broad flattened anterior wear facet. Enamel thickness varies up to 1·1 mm at the break on the buccal face, and although the tip of the crown is broken it appears to have been low-crowned. M 36370 is thus consistent in size and morphology with the other specimens of '*Sivapithecus africanus*'.

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A silicified brachiopod fauna from the Silurian of Iran

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Synopsis

A silicified brachiopod fauna has been recovered from a single bed in a limestone unit here named the Qarabil Limestone Formation, at the Robat-e-Qarabil inlier in the eastern Elburz Mountains, Iran. Twenty-three different articulate brachiopods are described, including one new genus, *Xerxespirifer* (Family Delthyridae), type species *X. iranicus* sp. nov., and two other new species, *Salopina brandi* and *Pentamerus asiaticus*. A probable Wenlock age is deduced.

Introduction

The Robat-e-Qarabil inlier lies to the north-east of Iran (Fig. 1), in the eastern Elburz Mountains, and was visited by the 1972 Oxford University Expedition to Iran, who made a geological map of the area, and also made extensive fossil collections, chiefly from the Devonian. The stratigraphy of the inlier has been briefly described by Brice *et al.* (1973 : 179), who described some of the brachiopod faunas, also chiefly from the Devonian; they list a succession, commencing with Horizon 1, 'Marnes calcaires et gréseuses à fragments de Brachiopodes et nombreux gros Polypiers', here termed the Qarabil Limestone Formation. This formation was measured by the Oxford Expedition as consisting of 52 m of limestones and interbedded marls with corals, which overlie the lavas and tuffs of an unnamed and undated formation beneath. The silicified fauna described in the present paper comes from a single bed 33 m above the base of the Qarabil Formation, 2½ km north-east of Robat-e-Qarabil; the bed is termed 'Lower Group 4' in the unpublished expedition report. Above the Qarabil Limestone Formation there is a stratigraphical break, which is followed by 90 m of thin limestones and marls with occasional sandstones (Horizons 2 and 3 of Brice *et al.* 1973), succeeded by 200 m of quartzites and shales, followed by a 1300 m sequence of clastic and carbonate rocks of largely Devonian age, many of which are richly fossiliferous (but they are not known to be silicified).

Age and affinities of the fauna

Many of the 23 different articulate brachiopods described below represent genera with a fairly wide age range within the Silurian; some also range down into the Ordovician and others up into

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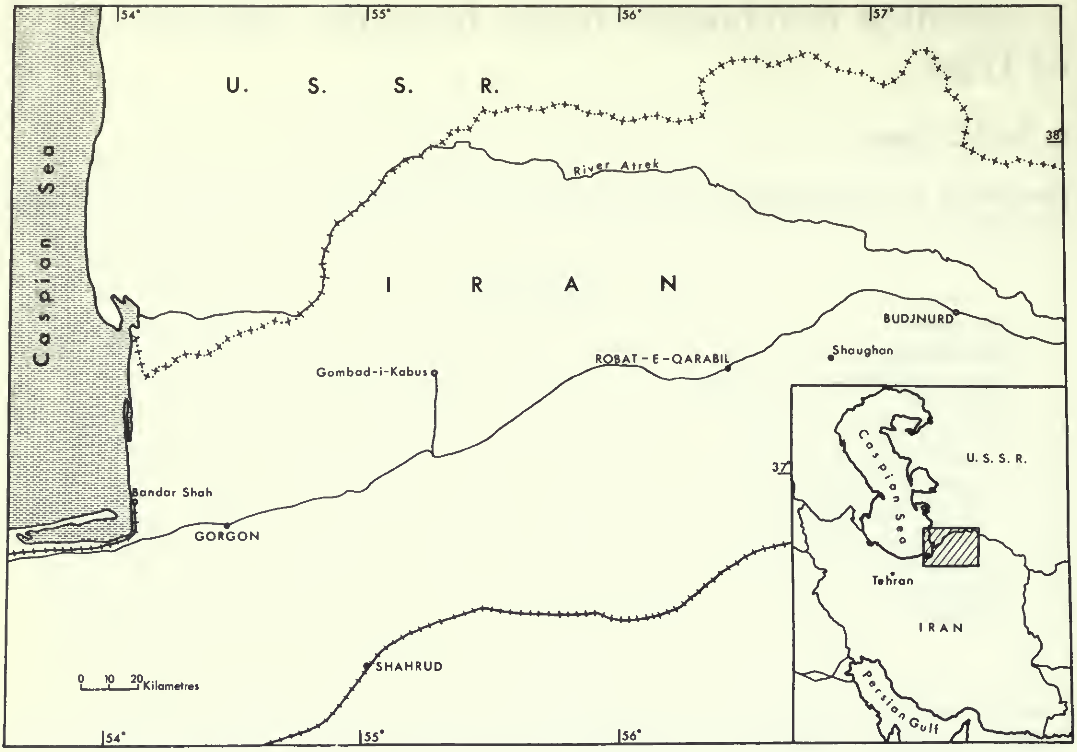


Fig. 1. The geographical position of the Robat-e-Qarabil inlier, Iran.

the Devonian, and there is no doubt that the age of the silicified fauna lies somewhere between the late Llandovery and the early Ludlow. The key forms in the more detailed assessment of age are as follows. *Glyptorthis* is not known from rocks younger than late Wenlock; *Epitomyonia* is not known from rocks younger than middle Wenlock; *Eoplectodonta* is most common in the early Silurian, and is not known from rocks younger than the middle Ludlow; *Shagamella* is not known from rocks earlier than late Wenlock; *Pentamerus* is most common in the Llandovery, and *P. asiaticus* sp. nov. is most like the pre-late Wenlock forms of the genus; *Plicoplasia* is not known from rocks older than the Ludlow; the large numbers of varied spiriferides present suggest an age later rather than earlier in the Silurian. Thus any age assessment would involve an extension of the range of at least some of the genera present, but a Wenlock age seems the most probable for the fauna as a whole, and probably the middle or later part of the Wenlock.

The associated fauna consists of fragments of the trilobite *Diacalymene*, kindly identified by Dr D. J. Siveter, the bivalve *Palaeoneilo*, kindly identified by Dr N. J. Morris, bryozoans, and the corals listed by Lafuste (*in* Brice *et al.* 1973 : 181), none of which contradicts the Wenlock age deduced from the brachiopods. No inarticulate brachiopods or graptolites are at present known from the Qarabil Formation.

The affinities of the fauna are puzzling. One of the most common brachiopods, *Xerxespirifer iranicus*, appears to be endemic, which is unusual in the middle Silurian, and the fauna is strikingly different from the roughly contemporary faunas described by Nikiforova (1937), and Sapelnikov & Rukavishnikova (1975) from the nearby southern parts of the Soviet Union. Dürkoop (1970) has partly described a fauna from central Afghanistan, which he ascribes to the Llandovery chiefly on the basis of an unillustrated *Pentamerus*, which may be comparable with the Iranian fauna.

It is not certain upon which continental plate Robat-e-Qarabil lay during Silurian times. In a recent reconstruction Ziegler *et al.* (1977) have extended the tentative boundary of Stöcklin (1974), which would place Robat-e-Qarabil on the southerly Gondwanan plate. However, this poses problems in that later Devonian and Jurassic faunas found to the north-east of Jarjarm, 50 km to the south-west of Robat-e-Qarabil, have a distinctly European as opposed to a Gondwanan aspect (Dr N. J. Morris, personal communication), which would indicate that the continental suture may have lain to the south, and that Robat-e-Qarabil would have been on the Kazakhstan plate. The question is unresolved, but if the new fauna were eventually found to have come from the Gondwanan plate then it would be of great interest, since no Silurian shelly faunas are known for over 3000 km to the west, or (apart from the possible Afghanistan fauna mentioned above) for a very long way to the east. Perhaps in Silurian times Robat-e-Qarabil lay on a smaller continental unit near the Gondwanan plate, which later drifted northwards.

Ecology

A total of 53 pairs of articulated valves, 143 disarticulated pedicle valves and 52 disarticulated brachial valves were recovered from the Lower Group 4 sample at Robat-e-Qarabil. However, of all the 23 different brachiopod species represented, only *Plicoplasia* sp. had a great disproportion of one valve to the other (no articulated specimens, 47 pedicle valves and 2 brachial valves), and, as argued below, this species was probably carried into the Lower Group 4 bed from elsewhere. When *Plicoplasia* sp. is therefore discounted, only five brachiopod species are present at over 5% of the total sample: *Salopina brandi* (26%), *Pentamerus asiaticus* (12%), *Lissatrypa* sp. (12%), *Eoplectodonta* aff. *bidecorata* (11%) and *Xerxespirifer iranicus* (10%); these five species together make up 71% of the total brachiopod fauna in the bed. The fauna is, however, a relatively diverse one, and probably indicates deposition under water that was not too shallow, perhaps comparable with the depth range of the *Pentamerus* or *Stricklandia* communities of the Llandovery of the Welsh Borderland (Ziegler, Cocks & Bambach 1968). This deduction is supported by the abundance of the associated coral fauna in Lower Group 4, since corals also reach their ecological acme in the *Pentamerus* and *Stricklandia* community depths. The relative abundance of spiriferides in the fauna also suggests a mid-shelf ecological position by comparison with the common mid-shelf spiriferide faunas of the later Silurian and the Upper Palaeozoic.

Systematic palaeontology

References to the authors of genera and species are given below in the list of references (p. 41), but those to the authors of higher taxa will be found in the *Treatise on Invertebrate Paleontology* (Williams *et al.* 1965).

Order **ORTHIDA** Schuchert & Cooper, 1932

Superfamily **ORTHACEA** Woodward, 1852

Family **HESPERORTHIDAE** Schuchert & Cooper, 1931

Subfamily **HESPERORTHINAE** Schuchert & Cooper, 1931

Genus ***HESPERORTHIS*** Schuchert & Cooper, 1931

Hesperorthis ? sp.
(Figs 4, 5)

MATERIAL. Two pedicle valves, BB 93340 (Fig. 5) and BB 93338, and two brachial valves, BB 93336 (Fig. 4) and BB 93339.

DIMENSIONS (in mm).	length	width
BB 93340, pedicle valve	18·8	*c.* 23
BB 93339, brachial valve	13·4	17·3

REMARKS. Although the pedicle valves are poorly preserved, they contain a suggestion of an apical plate in the delthyrium which indicates their attribution to *Hesperorthis*, in contrast to the open delthyrium of *Dolerorthis*. Chiang (1972) suggested that *Hesperorthis* should be confined to forms like the type species *H. tricenaria*, which possess only simple costae, as opposed to those like the Iranian form, whose costellae branch at mid-shell length (Fig. 5). These species with branched costellae, such as *H. gotlandica* and *H. martinssoni* from the upper Silurian of Gotland (Bassett & Cocks 1974 : pl. 1), have long been classified within *Hesperorthis*, but the differences observed by Chiang appear to be consistent from species to species, and hence this record of *Hesperorthis* is qualified by a query.

Subfamily **DOLERORTHINAE** Öpik, 1934

Genus ***DOLERORTHIS*** Schuchert & Cooper, 1931

Dolerorthis sp.

(Figs 2, 3)

Material. One pair of conjoined valves, BB 93341 (Fig. 2), and two pedicle valves, BB 93337 (Fig. 3) and BB 93349.

Dimensions (in mm).	length	width	thickness
BB 93341, conjoined valves	17·2	19.8	6·4
BB 93349, pedicle valve	18·4	*c.* 22	–

Remarks. Unfortunately the interior cannot be seen on any of the three specimens available, but the shape, ribbing, and open delthyrium and notothyrium are all typical of *Dolerorthis*, a genus which is well known and relatively common in rocks of Caradoc to early Devonian ages.

Subfamily **GLYPTORTHINAE** Schuchert & Cooper, 1931

Genus ***GLYPTORTHIS*** Foerste, 1914

Glyptorthis sp.

Material. Two small pairs of conjoined valves, BB 93391–92, two pedicle valves, BB 93348 and on BB 93405, and three brachial valves, BB 93345–7.

Dimensions (in mm).	length	width	thickness
BB 93391, conjoined valves	4·2	6·0	2·3
BB 93348, pedicle valve	5·5	7·8	–
BB 93346, brachial valve	10·1	*c.* 12	–

Remarks. *Glyptorthis* is rare in rocks of Silurian age, although *G. whitei* has been described by Bassett (1972) from the late Wenlock of Wales. The Iranian form differs from *G. whitei* in having relatively larger frilly growth lamellae which are also spaced further apart. In the pedicle valve interior the Welsh form has a raised muscle platform absent from the single Iranian pedicle interior.

Family **SCENIDIIDAE** Kozlowski, 1929

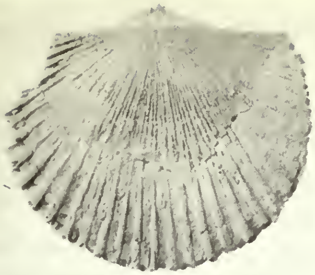
Genus ***SKENIDIOIDES*** Schuchert & Cooper, 1931

Skenidioides sp.

(Fig. 14)

Material. Three silicified pedicle valves, BB 93390 (Fig. 4), BB 93356–57.

Figs 2–11. Orthida from the Qarabil Limestone. (2, 3) *Dolerorthis* sp.; (2) BB 93341, conjoined valves viewed dorsally, laterally and ventrally, ×2; (3) BB 93337, pedicle valve, ×3. (4, 5) *Hesperorthis* ? sp.; (4) BB 93336, brachial valve interior, ×2; (5) BB 93340, pedicle valve exterior, ×1·5. (6–11) *Salopina brandi* sp. nov.; (6) BB 93333, **holotype**, conjoined valves viewed dorsally, laterally and ventrally, ×4; (7) BB 93334, a fragmentary brachial valve viewed externally and internally, ×4; (8) BB 93330, juvenile conjoined valves viewed dorsally and ventrally, ×4; (9) BB 93331, pedicle valve viewed externally and internally, ×4; (10) BB 93332, interior of a fragmentary pedicle valve, ×5; (11) BB 93335, brachial valve exterior, ×2.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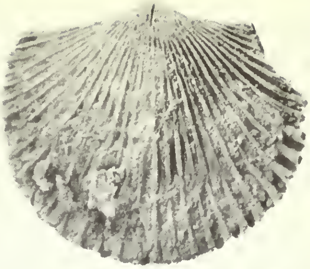
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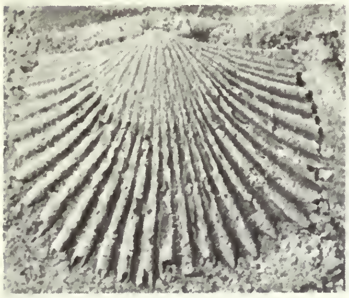
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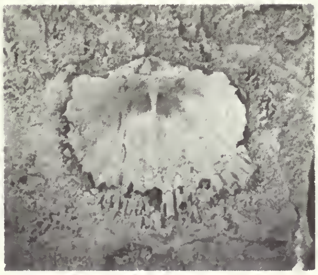
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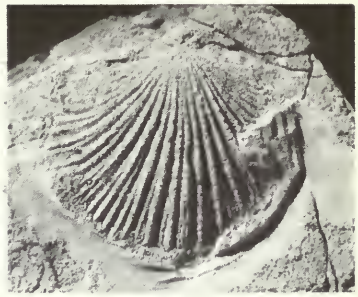
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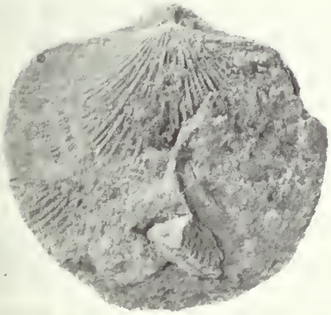
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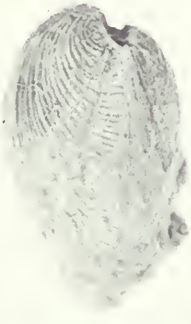
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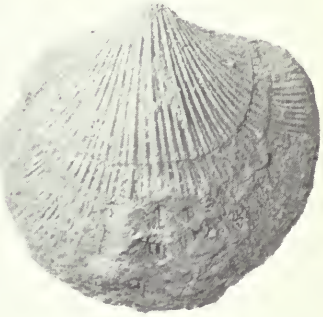
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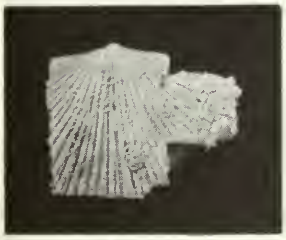
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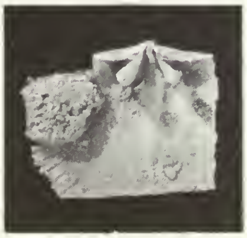
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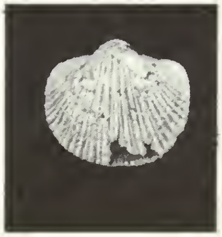
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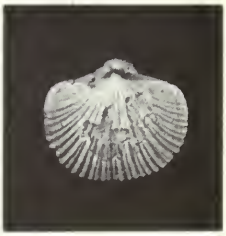
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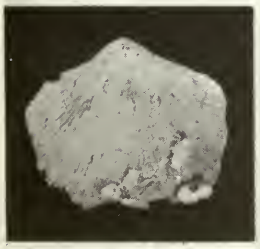
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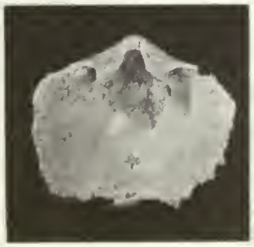
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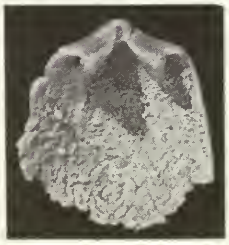
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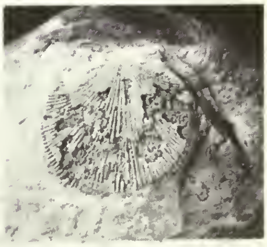
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Dimensions. All three valves have broken edges, but they are estimated to have been approximately 5 mm long and 6 mm wide when complete.

Remarks. There are many described species of *Skenidioides* from the Ordovician and Silurian (ten from Britain alone, Cocks 1978), and these fragmentary pedicle valves are best left under open nomenclature.

Superfamily **ENTELETACEA** Waagen, 1884

Family **SCHIZOPHORIIDAE** Schuchert, 1929

Subfamily **DRABOVIINAE** Havlíček, 1950

Genus *SALOPINA* Boucot, 1960

Salopina brandi sp. nov.

(Figs 6–11)

Diagnosis. Ventribiconvex *Salopina* with subcircular outline, weak dorsal sulcus, fine costellae and short, divergent brachiophores.

Description. *Exterior.* Ventribiconvex with subcircular outline. Weak sulcus on brachial valve. Hinge line relatively wider in juvenile individuals (Fig. 8). Small open delthyrium. Small curved apsacline pedicle interarea under incurved umbo, brachial valve interarea very small, with umbo scarcely developed. Ornament of fine costellae, hollow in cross-section. Prominent growth lines at irregular intervals.

Pedicle valve interior. Strong pair of teeth, supported by dental lamellae which merge with the valve floor posterior to the anterior end of the teeth. Muscle field weakly impressed and indistinct. Valve interior smooth, except at the periphery where the external costellae can be seen.

Brachial valve interior. Small, slender linear cardinal process. Strong brachiophores which also act as the anterior part of the socket. However, the brachiophores are relatively short for the genus and diverge from each other at approximately 90°. Muscle field of two pairs of adductor scars, separated centrally by a wide and shallow median ridge; the anterior pair larger than the posterior pair (Fig. 7b).

Material. Holotype BB 93333, conjoined valves (Fig. 6). Additional material: 7 other conjoined valves, including BB 93330 (Fig. 8) and BB 93353; 31 pedicle valves, including BB 93331–2 (Figs 9, 10), some fragmentary; 18 brachial valves, including BB 93334–5 (Figs 7, 11), some fragmentary, all from Lower Group 4, Robat-e-Qarabil inlier, Iran.

Dimensions (in mm).	length	width	thickness
BB 93333, conjoined valves (holotype)	9·9	10·3	5·9
BB 93330, conjoined valves	4·1	7·1	2·8
BB 93353, conjoined valves	5·8	7·4	3·4

Remarks. Walmsley *et al.* (1969) have given a useful review of the ten species which they ascribe to *Salopina* which had been described up to that time. From their table of specific differences, it can be seen that *Salopina brandi* falls into the group with relatively fine costellae, and it can be distinguished from other species with fine or medium costellae as follows. From *S. lunata* (J. de C. Sowerby, 1839), from the Ludlow of Britain, it differs in the shorter pedicle valve muscle field and the short divergent brachiophores; from *S. submedia* (McLearn, 1924), from the Telychian to Pridoli of North America, it differs in its convex brachial valve and shorter pedicle valve muscle field; from *S. conservatrix* (McLearn, 1924), from the Telychian to Eltonian of eastern North America and Europe, it differs in the valve outline, and also in the short divergent brachiophores, as opposed to the thin, erect to slightly convergent brachiophores of *S. conservatrix*; from *S. shelvensis* Walmsley, Boucott & Harper, 1969, from the Idwian of the Welsh Borderland, in the development of a dorsal sulcus, and once again in the distinctive brachiophores, which in *S. shelvensis* are thin and almost parallel. The subsequently-described (Johnson *et al.* 1976) species *S. delta* differs from *S. brandi* in possessing coarser costellae, a relatively wider hinge line, longer dental lamellae, and distinctive supporting plates to the brachiophore in the brachial valve.

Family **DICAELOSIIDAE** Cloud, 1948

Genus ***DICOELOSIA*** King, 1850
Dicoelosia sp.
(Fig. 12)

Material. One pair of conjoined valves, BB 93342 (Fig. 12), length 4·8 mm, width 4·6 mm, thickness 2·4 mm.

Remarks. The single specimen of *Dicoelosia* found in Lower Group 4 at Robat-e-Qarabil is relatively long, and similar in this respect to *D. verneuiliana* (Beecher) from the Telychian and Sheinwoodian of Gotland, Sweden (Wright 1968) and *D. alticavata* (Whittard & Barker) from the Telychian of Britain. It is also very indented at the anterior margin, which distinguishes it from *D. biloba* (Linnaeus), *D. paralata* Bassett, *D. osloensis* Wright, *D. oklahomensis* Amsden and from other species outside the Silurian. It is also relatively longer than *D. parvifrons* Johnson, Boucot & Murphy, and with its very concave brachial valve probably represents an undescribed species.

Genus ***EPITOMYONIA*** Wright, 1968
Epitomyonia aff. ***clausula*** Johnson, Boucot & Murphy, 1976
(Fig. 13)

Material. Three pairs of conjoined valves, BB 93344 (Fig. 13), BB 93345 and BB 93354, and one pedicle valve BB 93355.

Dimensions (in mm).	length	width	thickness
BB 93344, conjoined valves	3·4	3·9	1·9
BB 93345, conjoined valves	3·5	4·3	1·9
BB 93354, conjoined valves	2·6	3·5	1·4

Remarks. *Epitomyonia* was originally described from the Ashgill of Europe (Wright 1968), and is still not recorded from rocks of Llandovery age. However, it is now known by the species *E. clausula* from the Roberts Mountain Formation (Wenlock) of Nevada, U.S.A. (Johnson *et al.* 1976), and that species appears very similar to the scarce material from Iran, although the specific determination cannot be confirmed until internal details of the Iranian form are available.

Order **STROPHOMENIDA** Öpik, 1934

Superfamily **PLECTAMBONITACEA** Jones, 1928

Family **SOWERBYELLIDAE** Jones, 1928

Genus ***EOPLECTODONTA*** Kozlowski, 1929
Eoplectodonta aff. ***bidecorata*** (Barrande, 1879)
(Figs 16, 17)

Material. Three pairs of conjoined valves BB 93360, BB 93362, BB 93364; 13 pedicle valves, including BB 93361 (Fig. 17), BB 93363, BB 93365, BB 93367–8; and 13 brachial valves, including BB 93366 (Fig. 16), BB 93359, BB 93369–70.

Dimensions (in mm).	length	width
BB 93360, conjoined valves	10·4	*c.* 15·2
BB 93361, pedicle valve	5·6	10·3
BB 93362, pedicle valve	7·6	*c.* 15·5
BB 93366, brachial valve	6·9	12·5

Remarks. Cocks (1970 : 168) listed the late Silurian species of *Eoplectodonta*, which consist of *E. duvalii* (Davidson) from the Wenlock and Eltonian of Britain and Gotland, *E. sowerbyana* (Barrande) and *E. bidecorata* (Barrande), both from the Wenlock of Czechoslovakia, and possibly '*Sowerbyella*' *minuta* Kulkov from the late Wenlock of the Altai Highlands, Soviet Union.

'*S.*' *minuta* is poorly known, but differs from the Iranian form in its very wide spaces between the primary costae. *E. duvalii*, *E. sowerbyana*, *E. bidecorata* and the Iranian form are all very similar and clearly closely related to each other, except that *E. sowerbyana* has notably fewer costae than the rest (Havlíček 1967 : 60), and in fact the Iranian form is most similar to *E. bidecorata* in this respect, hence its tentative attribution. However, the Iranian form differs from *bidecorata* in at least two minor points, firstly in the common occurrence of low but prominent anterior plicae, which Havlíček describes as rare in *bidecorata*, and secondly by the development of a small but persistent median septum in the brachial valve (Fig. 16), consisting of scarcely more than a conjoined row of prominent tubercles. This septum has not been described or illustrated for *E. sowerbyana* or *E. bidecorata* by Havlíček (1967), but can be seen in the additional material of *sowerbyana* illustrated by Cocks (1970 : pl. 13, figs 5, 8) and also in the material of *E. duvalii* illustrated by Bassett (1974 : pl. 22, fig. 5), and perhaps occurred sporadically in all late Silurian populations of *Eoplectodonta*. However, its occurrence seems more prevalent in the Iranian form.

Superfamily **STROPHOMENACEA** King, 1846

Family **STROPHOMENIDAE** King, 1846

Subfamily **STROPHOMENINAE** King, 1846

Genus ***KATASTROPHOMENA*** Cocks, 1968

Katastrophomena sp.

Material. One pedicle valve, BB 93376, length 14 mm approx., width 19 mm approx., and one brachial valve, BB 93377, length 11·1 mm, width 17·8 mm.

Remarks. The interior of neither specimen is visible, but the shape and ornament of these valves are typical of *Katastrophomena*, which is known from the Ashgill to the early Ludlow of Europe and North America.

Subfamily **LEPTAENINAE** Hall & Clarke, 1893

Genus ***LEPTAENA*** Dalman, 1828

Leptaena sp.

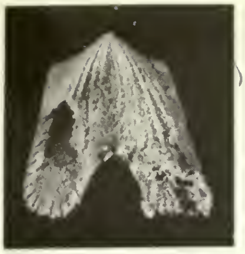
(Fig. 15)

Material. Two pedicle valves, BB 93371 (Fig. 15) and BB 93372.

Dimensions (in mm).	length of disc	length of trail	width
BB 93371, pedicle valve	8·3	7·3	*c.* 14
BB 93372, pedicle valve	7·5	4·1	*c.* 12

Remarks. This relatively small species of *Leptaena* is represented in the Iranian collection from Lower Group 4 by pedicle valves only. It is generally similar to a number of previously-described species, such as *L. ziegleri* and *L. purpurea* from the late Llandovery of the Welsh Borderland (Cocks 1968), but the outline of the disc and valve of the Iranian specimens is more rounded than the rather squarer or more quadrilateral outline of the British forms.

Figs 12–21. Orthida and Strophomenida from the Qarabil Limestone. (12) *Dicoelosia* sp., BB 93342, conjoined valves, viewed ventrally, dorsally and laterally, ×5. (13) *Epitomyonia* aff. *clausula*, BB 93344, conjoined valves viewed laterally and dorsally, ×5. (14) *Skenidioides* sp., BB 93390, pedicle valve interior, ×6. (15) *Leptaena* sp., BB 93371, pedicle valve exterior, interior, and viewed laterally, ×3. (16, 17) *Eoplectodonta* aff. *bidecorata*; (16) BB 93366, brachial valve interior, ×4; (17) BB 93361, pedicle valve exterior, ×4·5. (18) *Shagamella* ? sp., BB 93373, pedicle valve interior, ×5. (19) Chilidiopsid gen. et sp. nov., BB 93385, brachial valve interior and exterior, ×4. (20) *Coolinia* cf. *pecten*, BB 93383, brachial valve interior and exterior, ×9. (21) *Brachyprion* sp., BB 93378, pedicle valve interior, ×2.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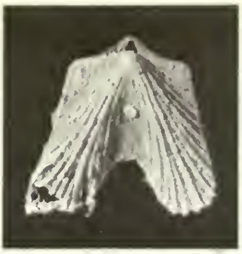
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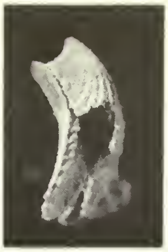
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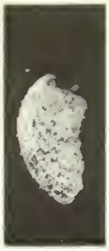
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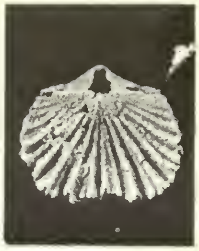
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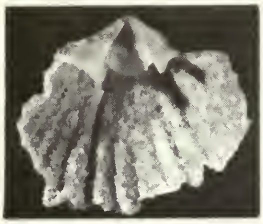
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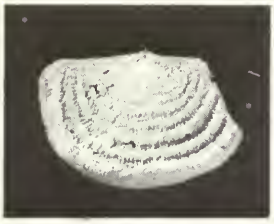
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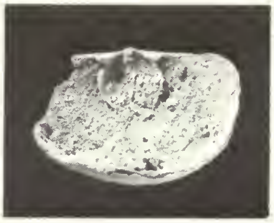
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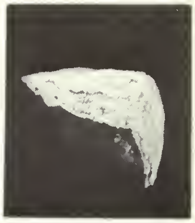
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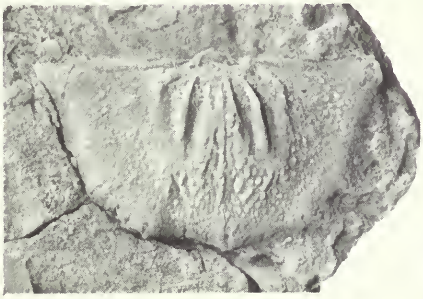
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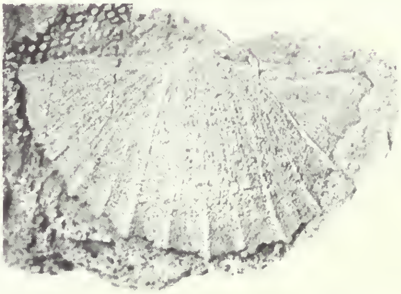
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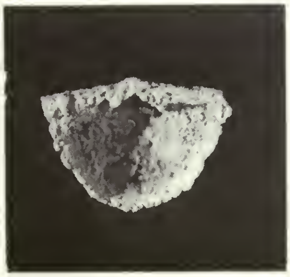
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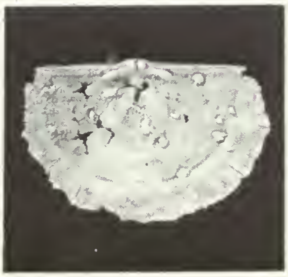
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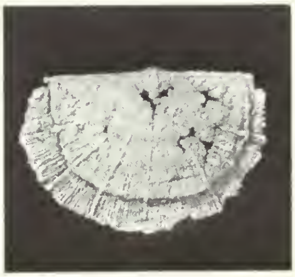
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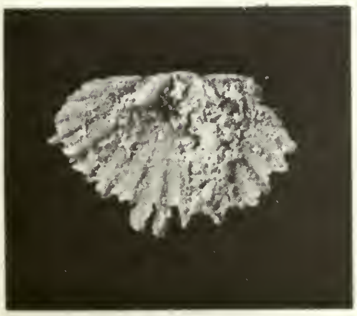
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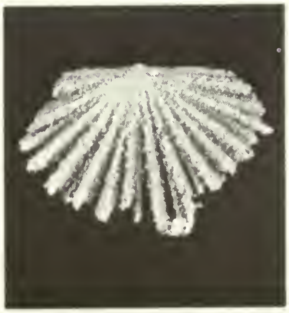
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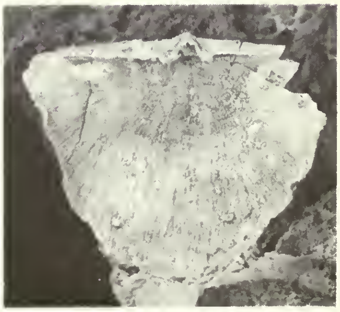

21

Family **STROPHEODONTIDAE** Caster, 1939

Genus ***BRACHYPRION*** Shaler, 1865
Brachyprion sp.
(Fig. 21)

MATERIAL. Two pedicle valves, BB 93378 (Fig. 21) and BB 93379.

DIMENSIONS (in mm).	length	width	height
BB 93378, pedicle valve	16·4	*c.* 22	*c.* 5
BB 93379, pedicle valve	14·1	*c.* 19	*c.* 5

REMARKS. The degree of convexity is not properly conveyed by the photograph (Fig. 21). This species of *Brachyprion* is very comparable with *B. arenaceus* from the late Llandovery of the Welsh Borderland (Cocks 1967).

Genus ***LEPTOSTROPHIA*** Hall & Clarke, 1892
Leptostrophia sp.

MATERIAL. Four pedicle valves, BB 93380–2 and on BB 93372.

DIMENSIONS (in mm).	length	width
BB 93380, pedicle valve	*c.* 10	*c.* 12
BB 93381, pedicle valve	3·9	*c.* 6

REMARKS. It is uncertain whether these four rather poorly preserved pedicle valves represent a small species of *Leptostrophia*, or whether they are juveniles. Their interiors show muscle fields typical of *Leptostrophia*, with muscle-bounding ridges diverging at approximately 70°. The ribbing style appears to be multicostellate, rather than the unequal parvicostellae more common in Silurian species of *Leptostrophia* (Cocks 1967).

Superfamily **DAVIDSONIACEA** King, 1850

Family **CHILIDIOPSIDAE** Boucot, 1959

Genus ***COOLINIA*** Bancroft, 1949
Coolinia cf. ***pecten*** (Linnaeus, 1758)
(Fig. 20)

MATERIAL. One brachial valve, BB 93383 (Fig. 20), and two pedicle valves, BB 93384 and on BB 93372.

REMARKS. All three specimens are fragmentary, not extending to the anterior or lateral margins, and the largest is preserved to a length of only 6 mm (large specimens of *Coolinia* from Europe reach lengths of over 40 mm). However, these small shells seem similar to the widespread *C. pecten*, which occurs abundantly in the Silurian of Sweden, Norway, Britain and Czechoslovakia.

Chilidiopsid gen. et sp. nov.
(Fig. 19)

MATERIAL. Two brachial valves, BB 93385 (Fig. 19) and BB 93386, and a fragment of pedicle valve, BB 93387.

DIMENSIONS (in mm).	length	width
BB 93385, brachial valve	5·2	7·1
BB 93386, brachial valve	5·1	*c.* 8

REMARKS. This species differs from other related and contemporary chilidiopsids, such as species of *Coolinia*, *Fardenia* and *Morinorhynchus*, in possessing an ornament of differentiated parvicostellae, not unlike the stropheodontid *Leptostrophia*. The only other Silurian chilidiopsid with such an ornament is *Valdaria*, but in that genus the costellae swing round to merge with the hinge-line laterally (Bassett & Cocks 1974 : pl. 5), and the socket ridges are poorly developed in contrast with the prominent very divergent socket plates of the Iranian form. The Robat-e-Qarabil brachial valves are very gently convex, and the single fragment of pedicle valve (which lacks the umbonal region) is rather more convex; it is not known whether the species is naturally small for the family, or whether the rare material is of juveniles. Unfortunately the small number of specimens to hand is inadequate to erect new generic and specific names.

Superfamily **CHONETACEA** Bronn, 1862

Family **ANOPLIIDAE** Muir-Wood, 1962

Genus ***SHAGAMELLA*** Boucot & Harper, 1968

Shagamella ? sp.

(Fig. 18)

MATERIAL. One pedicle valve, BB 93373 (Fig. 18).

DIMENSIONS. Length 3·5 mm, width 4·9 mm, height 1·9 mm.

REMARKS. The shape and form of this single valve recall *Shagamella*, which is known from the late Silurian of Britain and Venezuela (Boucot & Harper 1968). However, no spines can be seen on the valve edge, which is imperfectly preserved. A form approaching this is also seen in the contemporary plectambonitacean *Leangella*, but the distinctive muscle platform of the latter is not preserved on the Iranian specimen; hence the attribution to the anopliid.

Order **PENTAMERIDA** Schuchert & Cooper, 1931

Superfamily **PENTAMERACEA** M'Coy, 1844

Family **PENTAMERIDAE** M'Coy, 1844

Subfamily **PENTAMERINAE** M'Coy, 1844

Genus ***PENTAMERUS*** J. Sowerby, 1813

Pentamerus asiaticus sp. nov.

(Figs 22–26)

DIAGNOSIS. Very weakly trilobate *Pentamerus*, with relatively small and tightly incurved beak, and with relatively wide apical angles.

DESCRIPTION. Biconvex with weak trilobation, apical angle wide for the genus, approximately 90° for the pedicle valve and 110° for brachial valve. Pedicle umbo small and incurved (Fig. 22c), brachial umbo also small with orthocline interarea. Ornament absent, apart from growth lines. Pedicle valve interior has a simple spondylium and supporting septum (Fig. 24), extending to about valve mid-length. A deltidial plate is preserved. The brachial valve interior has discrete outer plates (Fig. 25), extending to just under valve mid-length in adult specimens.

MATERIAL. Holotype BB 93388, conjoined valves (Fig. 22). Additional material, one other pair of conjoined valves, BB 93396 (Fig. 26), 5 brachial valves, BB 93397–401, including BB 93399 (Fig. 25), and 16 pedicle valves, BB 93402 (Fig. 23), BB 93403 (Fig. 24) and BB 93404–17.

DIMENSIONS (in mm).	length	width	thickness
BB 93388, holotype, conjoined valves	47·3	48·2	22·1
BB 93397, brachial valve	–	61·4	21·5
BB 93404, pedicle valve	33·2	*c.* 37	18·0

REMARKS. The diagnosis separates *P. asiaticus* from the common Llandovery species *P. oblongus*, which is more trilobate; from the Wenlock *P. esthonus* (revised by Bassett 1977), which has a larger pedicle umbo and a relatively smaller cardinal margin; from *P. scalaris*, *P. subquadratus* and *P. issensis*, all from the Wenlock of the Urals (Sapelnikov 1972), by the small, tightly incurved umbo; from *P. longiseptatus* from the Llandovery of Kazakhstan and *P. oblongiformis* from the Ludlow of Kazakhstan, which both have a larger beak and narrower apical angle (Nikiforova

1937, Sapelnikov & Rukavishnikova 1975); from *P. magianicus* from the Lower Silurian of the Gornoi Altai (Menakova 1964) and Tian-Shan, which has several lobations and a narrower apical angle. There are also several nominal species of *Pentamerus* from North America, but these are either generically unrevised, junior synonyms of *P. oblongus*, or otherwise dissimilar to *P. asiaticus*.

Subfamily **CLORINDINAE** Rzonsnitskaya, 1956

Genus ***CLORINDA*** Barrande, 1879

Clorinda ? sp.

(Fig. 27)

Material. Two pedicle valves, BB 93418 (Fig. 27) and BB 93419.

Dimensions (in mm).	length	width	thickness
BB 93418, pedicle valve	12·1	*c.* 14	5·0
BB 93419, pedicle valve	*c.* 15	*c.* 18	4·7

Remarks. Since no brachial valves are available, the generic attribution must remain uncertain, but the form and structure of these two pedicle valves are consistent with *Clorinda* or *Brevilamula*.

Order **RHYNCHONELLIDA** Kuhn, 1949

Superfamily **RHYNCHONELLACEA** Gray, 1848

Family **TRIGONIRHYNCHIIDAE** Maclaren, 1965

Genus ***ROSTRICELLULA*** Ulrich & Cooper, 1942

Rostricellula sp.

Material. Seven articulated specimens, BB 93420–6, one other pedicle valve, BB 93427, and one other brachial valve, BB 93428.

Dimensions (in mm).	length	width	thickness
BB 93420, conjoined valves	4·6	4·8	1·9
BB 93421, conjoined valves	3·3	5·4	3·2

Remarks. These small sulcate rhynchonellaceans lack a cardinal process, precluding their inclusion in the two most common Silurian genera, *Stegerhynchus* and *Ferganella*. They are attributed here to *Rostricellula*, which lacks a cardinal process. It is not known whether these small specimens represent a small species, or whether they are juveniles.

Order **SPIRIFERIDA** Waagen, 1883

Superfamily **ATRYPACEA** Gill, 1871

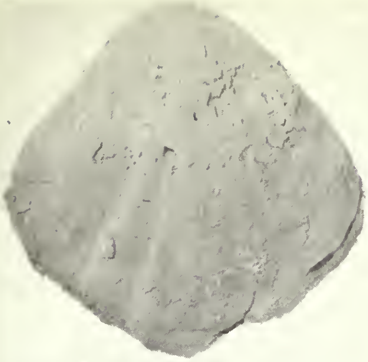
Family **ATRYPIDAE** Gill, 1871

Genus ***ATRYPA*** Dalman, 1828

Atrypa ? sp.

Material. Two pedicle valves, BB 93429, length 12·8 mm, width 14·4 mm, and BB 93430.

Figs 22–31. Pentamerida and Spiriferida from the Qarabil Limestone. (22–26) *Pentamerus asiaticus* sp. nov.; (22) BB 93388, **holotype**, conjoined valves viewed ventrally, dorsally and laterally, ×1; (23) BB 93402, pedicle valve viewed dorsally, ×1; (24) BB 93403, silicified pedicle valve showing the internal structures, ×2; (25) BB 93399, silicified brachial valve interior, ×5; (26) BB 93396, conjoined valves viewed ventrally and dorsally, ×2. (27) *Clorinda* sp., BB 93418, pedicle valve exterior, ×2. (28–31) *Lissatrypa* sp.; (28) BB 93431, conjoined valves viewed ventrally, dorsally, laterally and anteriorly, ×3; (29) BB 93447, pedicle valve interior, ×3; (30) BB 93432, broken conjoined valves viewed from the posterior showing spiralia, ×3; (31) BB 93443, broken conjoined valves viewed dorsally and laterally, showing spiralia and brachiophores, ×3.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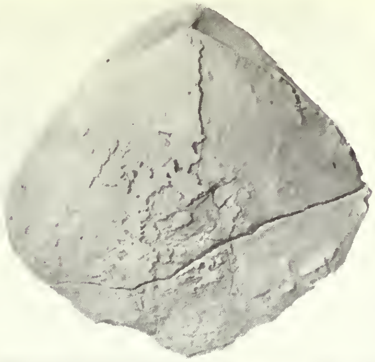
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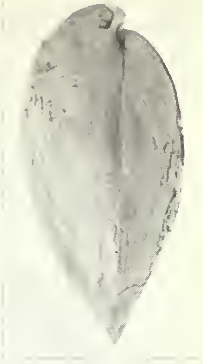
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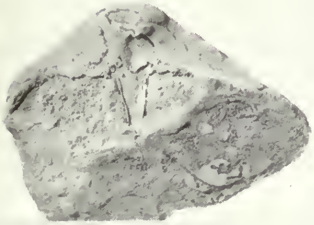
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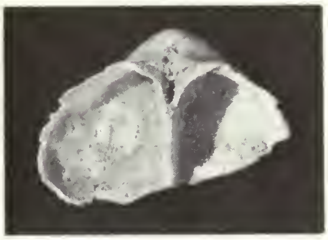
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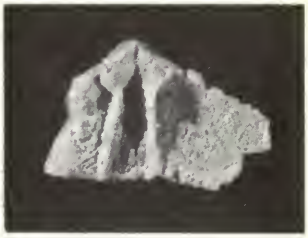
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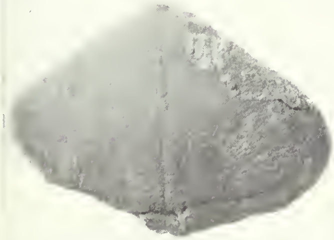
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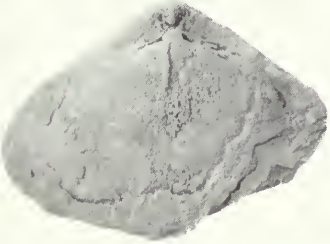
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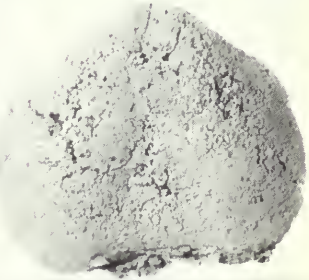
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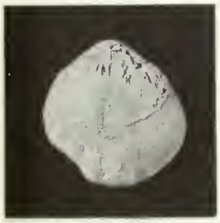
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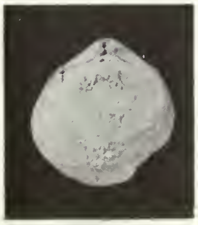
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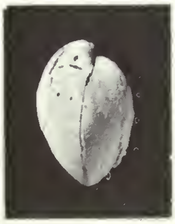
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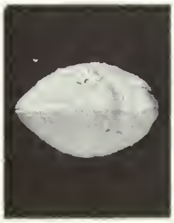
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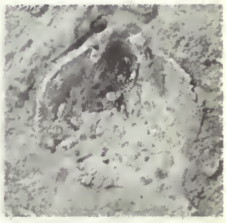
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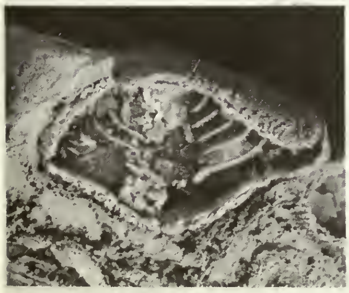
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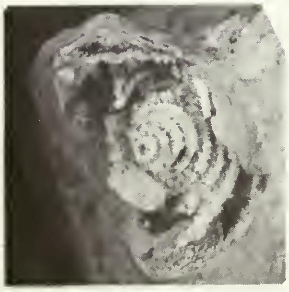
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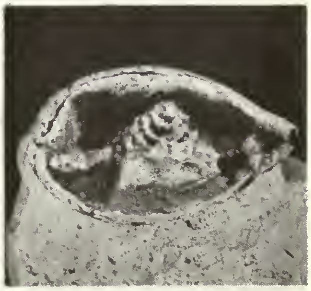

31b

REMARKS. Although certainly atrypid, the material is not sufficient for a positive generic attribution especially since the interiors are obscured by matrix. The growth lines are pronounced, even verging on frilly, over some of the costae.

Family **LISSATRYPIDAE** Twenhofel, 1914

Genus ***LISSATRYPA*** Twenhofel, 1914

Lissatrypa sp.
(Figs 28–31)

MATERIAL. Sixteen articulated individuals, BB 93431 (Fig. 28), BB 93432 (Fig. 30), BB 93433 (Fig. 31) and BB 93434–46, and one pedicle valve, BB 93447 (Fig. 29).

DIMENSIONS (in mm).	length	width	thickness
BB 93431, conjoined valves	9·8	9·3	6·3
BB 93439, conjoined valves	13·2	14·7	7·9

REMARKS. The internal structures have been delicately silicified in several of the specimens (Figs 30, 31), and the characteristic spiralia and brachiophores of *Lissatrypa* are clearly visible as set out in Copper (1973). Dr P. Copper has also seen the specimens and kindly confirmed the identification. However, only the two measured specimens are completely clear of matrix, and although the shape and form of BB 93439 is similar to *Lissatrypa atheroidea*, the type species from Anticosti Island, Canada (Twenhofel 1914 : pl. 1), the smaller specimen (Fig. 28) is proportionately thicker and less sulcate, which precludes specific identification of the Iranian form at present. *Lissatrypa* ? *sulcata* from Gotland differs in possessing a distinctive narrow median depression in both valves (Bassett & Cocks 1974 : pl. 9).

Superfamily **SPIRIFERACEA** King, 1846

Family **CYRTIIDAE** Fredericks, 1919

Genus ***EOSPIRIFER*** Schuchert, 1913

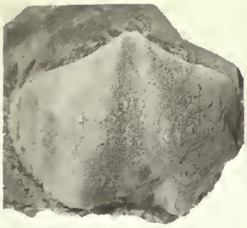
Eospirifer sp.
(Figs 32–33)

MATERIAL. Two pedicle valves, BB 93448 (Fig. 32) and BB 93449, and three brachial valves, BB 93450 (Fig. 33) and BB 93451–52.

DIMENSIONS (in mm).	length	width	thickness
BB 93448, pedicle valve	24·7	29·9	9·9
BB 93451, brachial valve	21·1	30·7	8·7

REMARKS. These finely-ribbed *Eospirifer* specimens have a more pronounced sulcus than the type species, *E. radiatus*, which is known from the late Llandovery to the Ludlow of Europe, North America and Asia. There is no hint of lateral ribbing on any of the material available.

Figs 32–41. Spiriferida from the Qarabil Limestone. (32, 33) *Eospirifer* sp.; (32) BB 93448, pedicle valve viewed ventrally and laterally, ×1; (33) BB 93450, broken brachial valve showing the exterior and the interior, ×3. (34–39) *Xerxespirifer iranicus* gen. et sp. nov.; (34) BB 93453, **holotype**, conjoined valves viewed dorsally, laterally and ventrally, ×3; (35) BB 93454, conjoined valves, ×3 – (35a) exterior viewed obliquely from anteroventrally, and (35b) interior with pedicle valve below, showing the distinctive muscle field, and a fragment of the brachial valve above; (36) BB 93464, pedicle valve exterior, ×2; (37) BB 93463, brachial valve exterior, ×2; (38) BB 93455, internal view of conjoined valves with brachial valve below and fragment of pedicle valve above, ×3; (39) BB 93462, brachial valve interior, with a small fragment of the pedicle valve attached to the posterior left of the hinge line, ×4·5. (40, 41) *Plicoplasia* sp.; (40) BB 93469 exterior, interior and lateral views of pedicle valve, ×5; (41) BB 93470, interior view of pedicle valve, ×4·5.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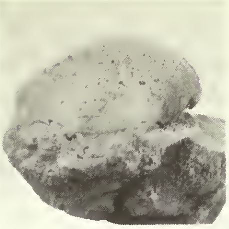
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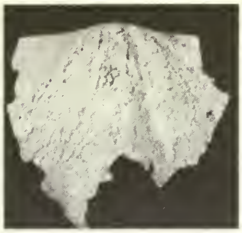
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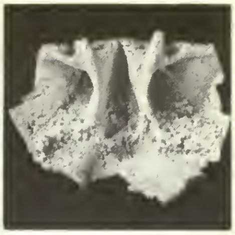
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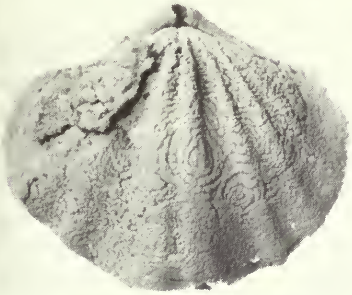
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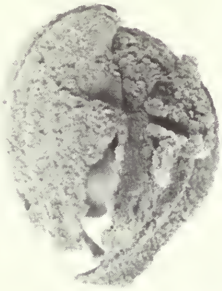
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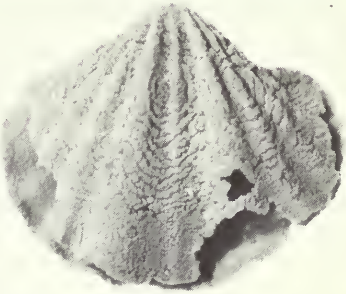
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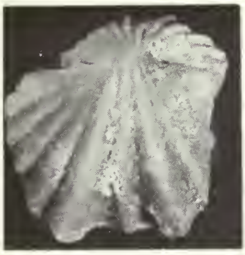
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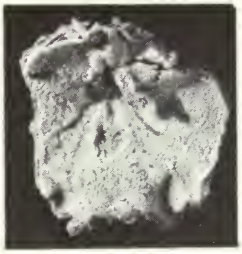
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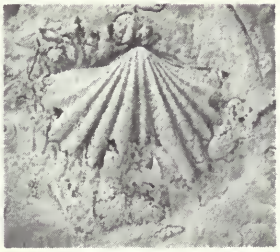
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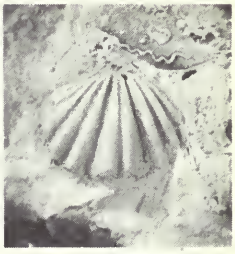
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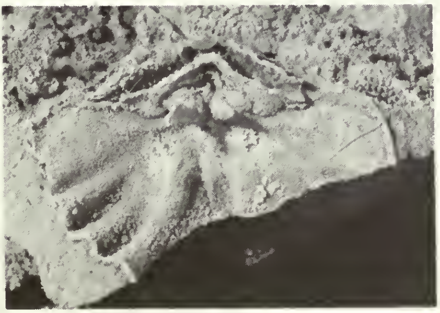
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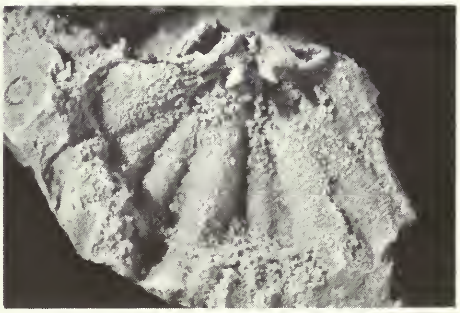
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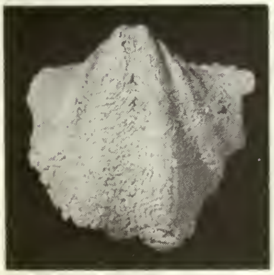
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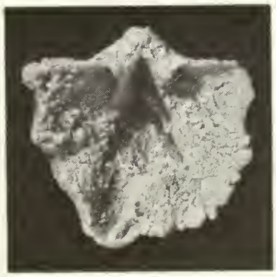
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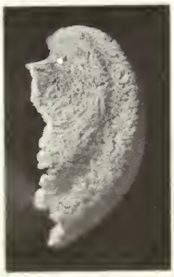
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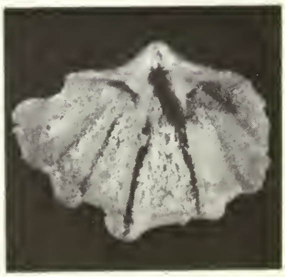
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Family **AMBOCOELIIDAE** George, 1931

Genus ***PLICOPLASIA*** Boucot, 1959

Plicoplasia sp.

(Figs 40–41)

Material. Forty-seven pedicle valves, including BB 93469 (Fig. 40), BB 93470 (Fig. 41) and BB 93471–98, many fragmentary, and two fragmentary brachial valves, BB 93499–500.

Dimensions (in mm).	length	width	thickness
BB 93472, pedicle valve	6·5	7·4	3·3
BB 93475, pedicle valve	6·3	7·7	3·4

Remarks. This chiefly Devonian genus has only recently been described from beds of Silurian age (Johnson *et al.* 1976 : 94), namely from the Ludlow of Nevada, U.S.A., the Wenlock of Arctic Canada and the Ludlow of Australia. The great numerical disproportion of pedicle over brachial valves in the Iranian sample suggests that these shells have been current-sorted and swept into the area of deposition from elsewhere; this is supported by the fact that nearly all the shells are broken anteriorly and laterally, where the valves are weaker.

Family **DELTHYRIDAE** Waagen, 1883

Subfamily **ACROSPIRIFERINAE** Termier & Termier, 1949

Genus ***XERXESPIRIFER*** nov.

Type species. *Xerxespirifer iranicus* sp. nov. (see below).

Diagnosis. Delthyrid like *Howellella* but with pinched-in pedicle muscle field, and with a median rib in the sulcus of the pedicle valve and a corresponding hollow in the brachial valve fold.

Remarks. In its characteristic median rib *Xerxespirifer* differs from *Howellella* in the same way as the kozlowskielline *Holcospirifer* differs from its relative *Boucotinskia*, and also as the eospiriferid *Nikiforovaena* differs from *Striispirifer* (for discussion see Bassett *et al.* 1976 : 620). The narrow width of the muscle field in the new genus is also a point of distinction from *Howellella*, as is also the more incurved beak. The presence of a small cardinal process is unusual in the Spiriferida.

Xerxespirifer iranicus sp. nov.

(Figs 34–39)

Description. *Exterior.* Ventribiconvex, with valves elliptical in outline, maximum width anterior to hinge line. Pedicle valve beak incurved, with interarea small, curved and apsacline, small open delthyrium, housing a presumably functional pedicle posteriorly. Brachial valve with very small interarea and almost imperceptible umbo. Radial ornament plicate, with ribs rounded in cross-section, with from three to six ribs on each flank; a small but distinctive median rib on the pedicle valve sulcus and a complementary trough on the fold in the brachial valve. Concentric ornament of fine growth lines.

Pedicle valve interior. Teeth small, but curved dorsoposteriorly (Fig. 35b), supported by small dental plates posteriorly only. There is no median septum. Muscle field well-impressed and pear-shaped, but narrow for the family, and extending less than half the valve length (Fig. 35b).

Brachial valve interior. Cardinal process small but distinct (Fig. 39). Sockets rounded, bounded anteriorly by curved socket plates which coalesce laterally with the hinge line. There is no median septum. Brachiophore bases short and stubby, protruding ventrolaterally at about 80° to each other just anterior to the cardinal process, but separated from each other by a small cavity. The form of the spiralia is unknown. Adductor muscle scars obscure, but perhaps represented by a pair of suboval areas at about valve mid-length (seen broken off in Fig. 38).

MATERIAL. Ten conjoined valves, including holotype BB 93453 (Fig. 34), BB 93454 (Fig. 35), BB 93455 (Fig. 38), BB 93456–61 and BB 93462 (Fig. 39), one other brachial valve, BB 93463 (Fig. 37), and 5 other pedicle valves, BB 93464 (Fig. 36) and BB 93465–8.

DIMENSIONS (in mm).	length	width	thickness
BB 93453, conjoined valves, holotype	9·3	11·1	7·6
BB 93456, conjoined valves	13·2	16·1	10·8
BB 93459, conjoined valves	*c.* 12	13·7	*c.* 9

REMARKS. The Iranian material described here as *X. iranicus* is the only material so far known which can be ascribed to *Xerxespirifer*. Whether or not the new genus is truly endemic to Iran is not yet known. *X. iranicus* is almost certainly the same form as that identified as *Platystrophia* sp. by Brice *et al.* (1973 : 183; pl. 21, fig. 13), but whose internal structures were then unknown.

Acknowledgements

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Two new condylarths (Mammalia) from the early Eocene of southern England

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Synopsis

Hyopsodus wardi sp. nov. is described as the first English species of the mainly North American genus *Hyopsodus* and is shown to be closely related to the earliest North American species *H. loomisi. Lessnessina packmani* gen. et sp. nov. is described, extending the range of the anisonchine Periptychidae from exclusively the Palaeocene of North America into the early Eocene of Europe.

Introduction

Collecting over the past two decades in the early Eocene Blackheath Beds of Abbey Wood (London Borough of Bexley) has brought to light a number of mammalian specimens. Amongst these are several jaw fragments and isolated teeth representing two new species of condylarth. One belongs to *Hyopsodus* Leidy, the other to a new monotypic genus. The new *Hyopsodus* specimens have allowed this genus to be recognized in older collections from Abbey Wood and from the Suffolk Pebble Beds (early Eocene) of Kyson, Suffolk, where it had been misidentified. Most previous European records of *Hyopsodus* (Rütimeyer 1892, Teilhard de Chardin & Fraipont 1921) belong to other taxa (see Stehlin 1906 : 632–634; and below). Russell (1968) was the first to record the genus from Europe correctly; Dashzeveg (1977) has described an endemic species from Mongolia.

A relatively small number of mammalian species have already been described from Abbey Wood (White 1931, Cooper 1932*a*, *b*, Simons 1962, Van Valen 1965, Kühne 1969) but recent collecting by bulk sampling, sieving and acetic acid concentration has begun to provide glimpses of a much larger fauna. Remains are sparse and often fragmentary, but the taxa described here are among the best-represented so far. Stratigraphical details of various temporary sections dug in the Blackheath Beds of Abbey Wood appear in Epps & Priest (1933), Rundle (1970; contains numerous additional references), Ward & Cooper (1971) and Hooker (1975). Two lithostratigraphic terms (Lessness Shell Bed and Abbey Wood Member) introduced by Cooper (1976 : 6) are used here but are included in the Blackheath Beds (informal usage) contrary to Cooper's interpretation.

Material and abbreviations. Nearly all the specimens described here are in the Department of Palaeontology, British Museum (Natural History); their numbers are prefixed M. Those of other collections are prefixed as follows: University of California (UC); University of Michigan (UM); W. Morris private collection (MC).

The initials of the collectors are indicated where relevant: Messrs S. A. Baldwin, A. G. Davis, F. J. Epps, W. George, P. R. Gurr, J. J. Hooker, R. G. Maynard, A. R. G. Packman and D. J. Ward.

l=maximum length; w=maximum width (w_1 and w_2 being widths of trigonid and talonid respectively of lower teeth); L=left; R=right.

Systematic descriptions

Order **CONDYLARTHRA** Cope, 1881

Family **HYOPSODONTIDAE** Trouessart, 1879

Genus ***HYOPSODUS*** Leidy, 1870

TYPE-SPECIES. *Hyopsodus paulus* Leidy, 1870; Bridgerian, Middle Eocene, Wyoming, U.S.A.

Bull. Br. Mus. nat. Hist. (Geol.) **32** (1) 43–56. Issued 28 June 1979

Hyopsodus wardi sp. nov.
Figs 1–6; 8–13

HOLOTYPE. Right maxillary fragment with P^4 alveoli and M^{1-2} (M 29762).

PARATYPES. Twenty-four jaw fragments and isolated teeth listed in Table 1.

DERIVATION OF NAME. Named after Mr D. J. Ward, who collected the holotype.

TYPE HORIZON AND LOCALITY. Lessness Shell Bed within the lower sandy Abbey Wood Member of the Blackheath Beds, Sparnacian, early Eocene; the sandpit, Abbey Wood, London Borough of Bexley (National grid TQ 480786).

RANGE. Apart from specimens from the type locality, two isolated teeth of *Hyopsodus* from the Suffolk Pebble Beds of Kyson, Suffolk (TM 269475), may represent this species and are referred to as *H.* cf. *wardi.*

DIAGNOSIS. *Upper molars*: short and broad; ectocingula variably developed; M^{1-2} hypocones small and close to protocones; protostyles present; M^3 triangular and without hypocone.

Lower molars: short and broad; relatively transverse orientation of opposing buccal and lingual cusps; paraconid prominent and may be isolated from metaconid on M_1, small and close to metaconid on M_2; talonid notch narrow and with entoconulid; entoconid notch (*sensu* Gingerich & Simons 1977) very shallow.

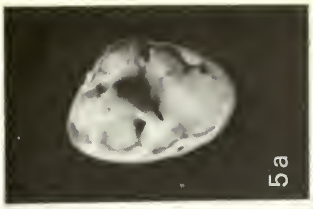
These characters distinguish *H. wardi* from all described species of *Hyopsodus* except *H. loomisi* McKenna, 1960; this is larger (Fig. 14; Table 1) but morphologically similar, except that it completely lacks upper molar ectocingula. Mean length of *H. wardi* M^2 is 2·90 mm.

DESCRIPTION AND COMPARISONS. (Dental terminology follows Van Valen (1966) and Szalay (1969) except that upper mesial and distal cingula are not separated into para- and precingula and meta- and postcingula respectively.)

Size has been shown to be the only reliable character to differentiate contemporaneous species of North American *Hyopsodus* which are otherwise morphologically identical (Gingerich 1976). Morphology in the genus, however, changes with time. Dimensions of the few known upper teeth of *H. wardi* do not overlap with those of the holotype of *H. loomisi*, according to McKenna's (1960 : 106) measurements (see Fig. 14). Those of more extensive assemblages of both species would almost certainly overlap slightly. M 29640, the buccal half of a left M^1, assuming that the other three M^1s are near the mean, must be close to the upper size limit for *H. wardi.* There is the slight possibility that M 29640 belongs to a larger species of *Hyopsodus* occurring alongside *H. wardi*, but more material is obviously needed to decide this. Apart from the measurements of the holotype, Guthrie (1967 : 38, text-fig. 27) has produced a histogram with measurements of two M_2s of *H. loomisi* from Four Mile, Colorado (the type locality), which almost fit within the range of those of *H. wardi* M_2s. However, *H.* '*miticulus*' also from Four Mile (see measurements in McKenna, 1960 : table 6) may also refer to *H. loomisi* (personal communication, Dr P. D. Gingerich). If Guthrie's (1967) measurements of *H.* '*miticulus*' from Four Mile are thus included with those of *H. loomisi*, the supposed bimodality not being obvious, the mean M_2 length is increased. This mean measure conforms more closely to that expected from the upper tooth measurements of the holotype of *H. loomisi*, and is thus greater than that of *H. wardi*. Gingerich (1976 : text-figs 4–5) has provided statistical measurements of M_1 for a sequence of assemblages in the Big Horn Basin, Wyoming, identified as *H. loomisi*, which range fairly widely in size, but would encompass those of the holotype. The stratigraphically lowest of these (1976: text-fig. 5) would overlap considerably with *H. wardi*.

Figs 1–6. *Hyopsodus wardi* sp. nov. from the Blackheath Beds of Abbey Wood; upper teeth. Fig. 1, LP^2, M 32167. Fig. 2, RP^3 (reversed), M 31997. Fig. 3, LP^4, MC 44. Fig. 4, **holotype** R maxilla with P^4 alveoli and M^{1-2} (reversed), M 29762. Fig. 5, RM^3 (reversed), M 29644. Fig. 6, LdP^3, M 29745. 'a' suffixes are occlusal views; 'b' suffixes are buccal views.

Fig. 7. *Lessnessina packmani* gen. et sp. nov. from the Blackheath Beds of Abbey Wood; RM^1, MC 17; a, buccal view; b, occlusal view. All specimens ×6 and sprayed with ammonium chloride.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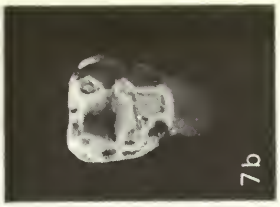
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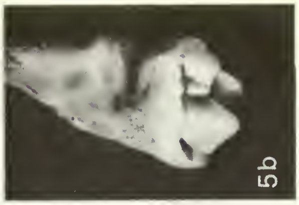
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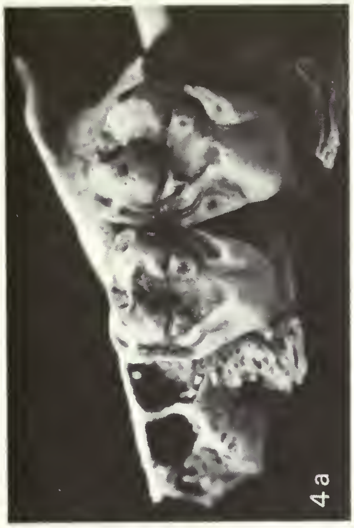
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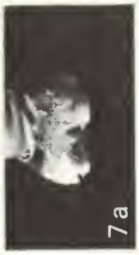
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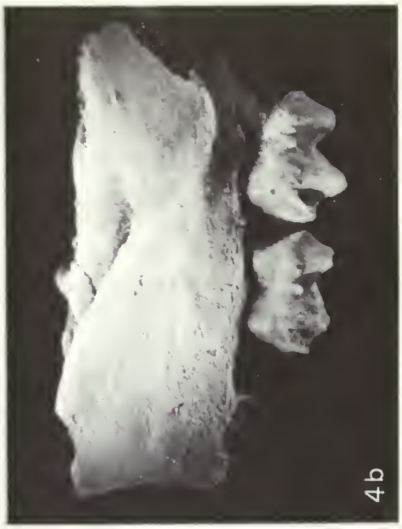
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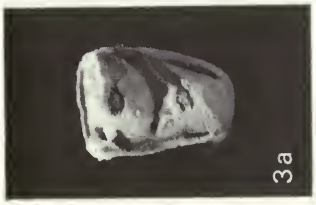
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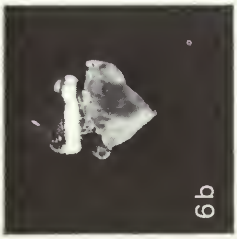
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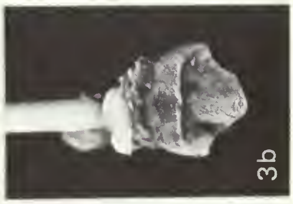
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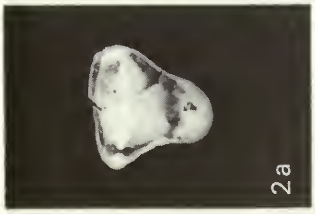
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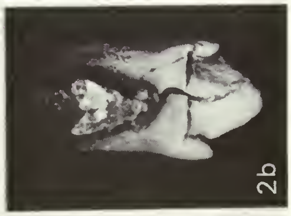
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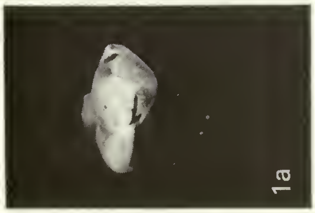
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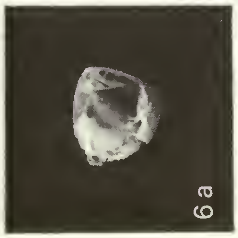
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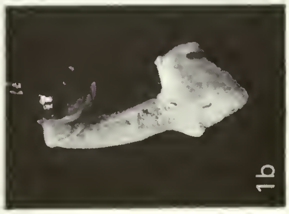
1b

P^2 (M 32167) is almost identical in morphology to that of the holotype of *H. loomisi* (UC 44781; McKenna 1960 : 107, text-fig. 58).

P^3 is triangular in outline. M 29408 appears relatively slightly shorter than M 31997, even accepting the broken-off parastyle. The mesiolingual and distolingual margins are slightly concave in M 31997, straight in M 29408. The distal cingulum continues lingually beyond the junction with the postprotocrista in M 29408, but stops at the junction in M 31997. The buccal margin is slightly convex in M 31997, straight in M 29408. M 31997 has a very slight lingual bulge on the postparacrista which suggests an incipient metacone, absent in M 29408. The mesial cingulum in both specimens projects lingually beyond the junction with the preprotocrista. In the holotype of *H. loomisi* the mesial cingulum and preprotocrista form a single crest. In outline shape, of the two Abbey Wood P^3s M 29408 is more like the holotype of *H. loomisi*, whilst M 31997 is more like a referred specimen of *H. loomisi* (UM 63620) from Locality 383 of the Bighorn Basin. Thus at least one type of individual variation of *H. loomisi* is paralleled by *H. wardi*.

Of the two P^4s, MC 44 is complete and MC 65 is a protoconal fragment. Outline shape of MC 44 is very similar to that of the holotype of *H. loomisi* (UC 44781). Mesial and distal cingula on both have the same lingual extent as in UC 44781. The ectocingulum is complete in MC 44, missing in UC 44781. Presence of a small metacone on MC 44 is suggested by a lingual dentine bulge behind the paracone, unlike UC44781. There is a very small paraconule on MC 44 but not on MC 65. It is missing in McKenna's (1960) figure of UC 44781. The last two features appear to have only individual significance, being variable in different North American *Hyopsodus* species.

The dP^3 (M 29745) has a broken mesial edge. It is much smaller than the two P^3s, more quadrate in outline, relatively lower-crowned, with a very small metacone and no metastyle. Deciduous premolars of *Hyopsodus* appear to be uncommon in North America. Gazin (1968 : 50; pl. 6, fig. 3) figured the 'best-preserved': dP^{2-4} of *H. lepidus* Matthew, 1909 from the Bridger Formation of the Green River Basin, Wyoming. Compared to dP^3 in the figure, M 29745 was apparently less tapered mesially and the distobuccal corner is slightly acute instead of right-angled; the figure is not detailed enough for further comparisons. The size ratios of dP^3 to permanent teeth in *H. wardi* are similar to those of *H. lepidus* as shown by Gazin's illustrations (1968 : pl. 6, fig. 3 and pl. 7, fig. 3).

On the upper molars, there is variation in development of the ectocingulum but on the available specimens it is never completely absent as it is on the holotype of *H. loomisi*. McKenna (1960 : 106) used this as a diagnostic character of the latter species. Possible variation in upper molar characters such as development of the hypocone and ectocingulum attributed to *H. loomisi* by Gazin (1962 : 62) refer to assemblages away from the type area of the species and they *may* not be referable to *H. loomisi*. Some of the problems have been discussed by Delson (1971 : 350–351). Most of the upper molars of *H. wardi* have an incipient mesostyle either in the form of a vertical ridge on the buccal wall or a denticle on the ectocingulum. The paraconule and metaconule cristae show much variation in development. There is variation in the buccal saliency of the paraconal region in M^2 and M^3. M^3 varies more than M^2 in size, proportions and degree of reduction of the metacone. The distal cingulum on M^3 is also variable, in M 29631 there being at its lingual end a minute denticle in the position of a hypocone.

McKenna (1960) could find little significant to write about the lower teeth of *H. loomisi* and did not figure them. For comparison with *H. wardi* I have relied on referred material: a cast of UM 63621 from Locality 383, Bighorn Basin and figures in Gazin (1962 : pl. 9, figs 5–7) of specimens from Bitter Creek, Washakie Basin, Wyoming. The P_3s and P_4 from Abbey Wood are similar to these teeth in UM 63621 but the trigonids are slightly more open and the paraconids

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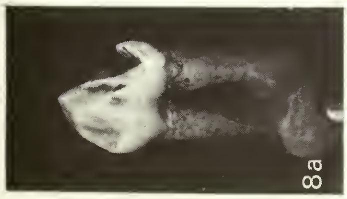
Figs 8–13. *Hyopsodus wardi* sp. nov. from the Blackheath Beds of Abbey Wood; lower teeth. Fig. 8, RP_3, M 15126. Fig. 9, RP_4, M 29757. Fig. 10, RM_1, M 15123. Fig. 11, LM_2 (reversed), M 29497. Fig. 12, fragment of R mandibular ramus with M_3, M 15132. Fig. 13, fragment of R mandibular ramus with M_{1-2}, M 15146, in buccal view. 'a' suffixes are lingual views; 'b' suffixes are occlusal views; 'c' suffixes are buccal views. All specimens ×6 and sprayed with ammonium chloride.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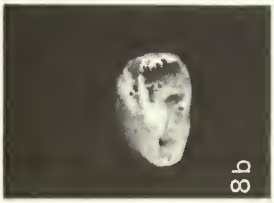
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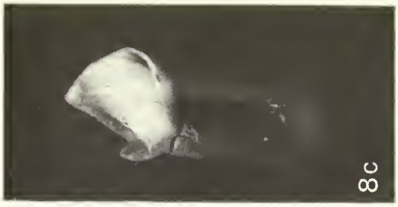
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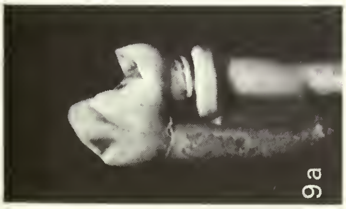
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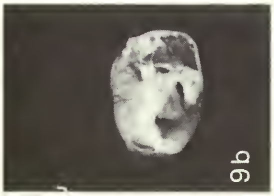
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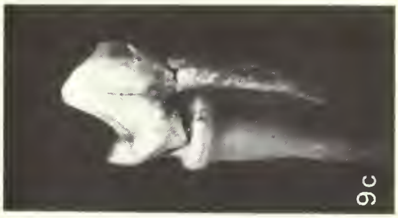
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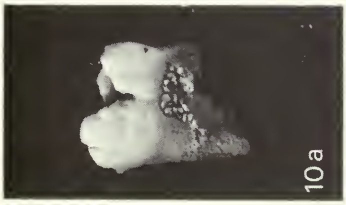
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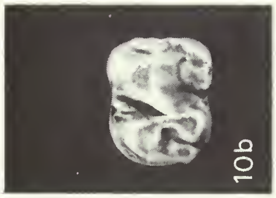
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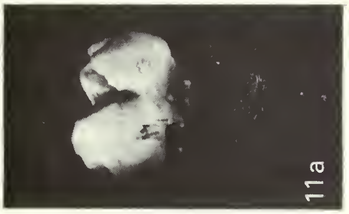
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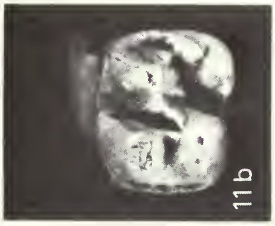
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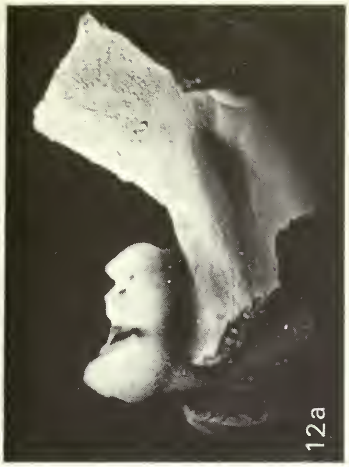
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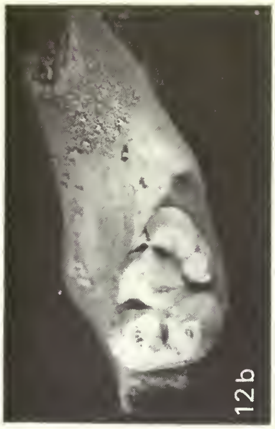
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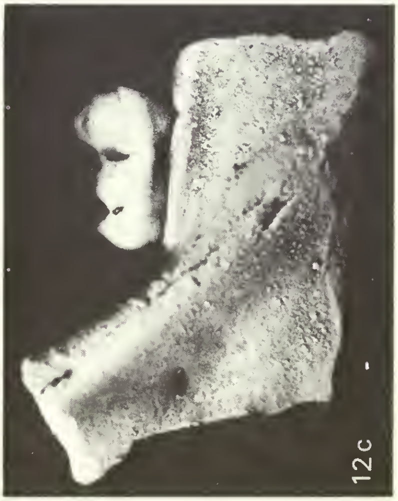
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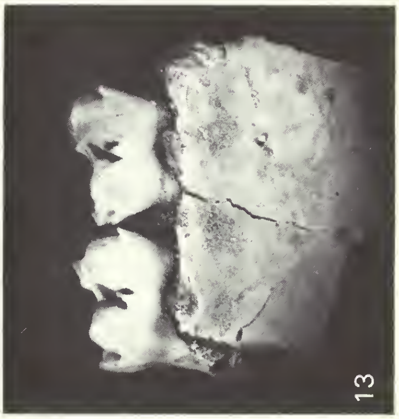
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and metaconids smaller. There is a closer resemblance to one of the Bitter Creek specimens (Gazin 1962 : pl. 9, fig. 6).

H. wardi lower molars are very similar to those of UM 63621 and the Bitter Creek specimens except that the crest joining the entoconid and hypoconulid is more prominent, causing these cusps to be less separated (i.e. very shallow entoconid notch). The M_1 paraconids seem a little less distinct in the Bitter Creek specimens than in *H. wardi*. Of the two *H. wardi* M_1s, one (M 15123) has a distinct paraconid isolated from the metaconid; the other (M 15146), although at a similar wear stage, has a smaller paraconid fused to the metaconid. All the sufficiently well preserved lower molars have entoconulids (= entostylids); some have transversely elongated ectostylids unlike UM 63621. The M_3 (M 15132) has a more distally tapering talonid than UM 63621 and, unlike the latter, a buccal cingulum round the protoconid.

Only one specimen of *H. wardi* has M_1 and M_2 associated. The isolated M 15123 on the one hand and M 29497 and M 29698 on the other can, however, be confidently identified as M_1 and M_2 respectively. The former has a distinct paraconid and the talonid wider than the trigonid, whilst the latter two have very small paraconids close to the metaconids and talonids equal to or narrower than the trigonids. The other known preultimate molars are too worn or broken to be further identified.

H. orientalis Dashzeveg 1977, from the early Eocene of Naran Bulak, Mongolia, has been diagnosed as having M^2 significantly larger than M^3; hypocone absent on M^3; lower molars with well-developed paralophid and weak entoconid from which lingual hypoconulid is weakly separated. The size ratios between some of the M^1s and M^2s seem more significant than between M^2 and M^3, but not in every case (judged from Dashzeveg's figures and measurements). In addition, the M^{1-2} centrocristae are acutely buccally flexed, the M^{1-2} parastyles are prominent and, according to the figures, the lower cheek teeth appear higher-crowned than in other *Hyopsodus* species. The M_1 paraconid is stated to be present but appears much smaller than in *H. wardi*. Apart from the obvious differences *H. orientalis* is slightly smaller than *H. wardi* although the measurements overlap.

Table 1. Length and width measurements (mm to nearest 0·05) of English *Hyopsodus wardi* sp. nov. (including *H.* cf. *wardi*.). Brackets indicate an estimate. Only a single width measurement is given for lower premolars

Number	Tooth	l.	w.	Number	Tooth	l.	w_1	w_2
UPPER DENTITION				LOWER DENTITION				
M 32167 (RGM)	LP^2	2·00	1·45	M 15126 (FJE)	RP$_3$	2·45	1·75	
M 29408 (JJH)	RP^3	–	2·70	MC 133	LP$_3$	2·45	1·75	
M 31997 (JJH)	RP^3	2·65	2·60	M 29757 (SAB)	RP$_4$	2·75	2·00	
MC 44	LP^4	2·40	3·40	M 15146 (AGD)	RM$_1$	3·05	2·30	(2·45)
MC 65	LP^4	–	–		RM$_2$	3·15	2·60	2·60
M 29762 (DJW)	RM^1	2·65	3·40	M 15123 (FJE)	RM$_1$	2·85	2·20	2·30
(holotype)	RM^2	2·90	4·00	M 29497 (WG)	LM$_2$	3·50	(2·90)	(2·90)
M 29631 (ARGP)	LM^2	2·80	4·10	M 13766 (FJE)	RM$_{1/2}$	3·30	2·55	–
	LM^3	2·30	3·35	M 13767 (FJE)	RM$_{1/2}$	3·10	–	–
M 20214 (PRG)	LM^1	2·70	3·40	M 31881 (SAB)	RM$_{1/2}$	3·10	–	–
M 29640 (PRG)	LM^1	3·05	–	M 15132 (AGD)	RM$_3$	3·40	2·55	2·10
M 29642 (PRG)	LM^1	2·75	3·45					
M 20218 (PRG)	LM^2	3·15	4·30					
M 29643 (PRG)	RM^2	2·90	3·90	M 29698*	RM$_2$	3·25	2·65	2·40
M 29644 (PRG)	RM^3	2·15	3·20					
M 32144 (JJH)	RM^3	2·15	3·20					
M 29745 (SAB)	LdP^3	–	2·05					
M 29694*	RM^2	2·90	4·45					

**Hyopsodus* cf. *wardi*; not paratypes.

The holotype right maxilla of *H. wardi* is truncated anteriorly at the level of the infraorbital foramen which forms part of the edge. It lies above the former position of the distal half of P^3. The orbital floor is preserved with the opening of the maxillary canal above the junction of P^4 (now missing) and M^1. The base of the zygomatic arch is opposite M^2. M 29631 is a left maxilla which shows the base of the zygomatic arch and part of the orbital floor.

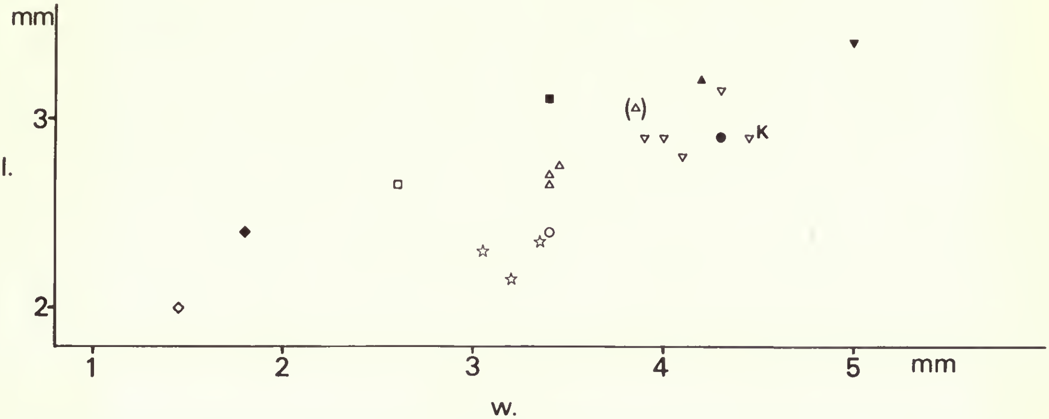

Fig. 14. Scatter diagram of length versus width for upper cheek teeth of *Hyopsodus wardi* sp. nov. (hollow symbols) and of the holotype of *H. loomisi* McKenna (after McKenna 1960) (solid symbols). ◇◆ = P^2; □■ = P^3; ○● = P^4; △▲ = M^1; ▽▼ = M^2; ☆ = M^3. K indicates *H.* cf. *wardi* from Kyson. Brackets indicate that the width is estimated.

DISCUSSION. It has been shown above that *H. wardi* is very similar to *H. loomisi*. If North American and English *Hyopsodus* evolved in parallel at the same rate, then the best transatlantic correlation of the Blackheath Beds of Abbey Wood would be with strata in the Rocky Mountains belonging to the Lower Graybullian land mammal age within the early Wasatchian (early Eocene). Savage (1971) pointed out the great similarities between the Sparnacian mammal faunas of north-west Europe and those of the early Wasatchian of Wyoming. He noted that c. 60% of the genera found in Europe were identifiable in North America. This is even more than in the Pleistocene, when glaciations favoured circumpolar ranges, or in the immediately preceding Palaeocene. He suggested that the similarities reflect a sudden migration across the area. In a migration of this kind one would expect even the species to be identical, but this does not appear to be so. This may be because the basal Sparnacian fauna of the Conglomérat de Meudon is poorly known and the main Sparnacian faunas are from higher horizons.

Gingerich (1977 : 63) has pointed out that the European adapid primate *Pelycodus eppsi* (C. F. Cooper) from Abbey Wood differs from all North American *Pelycodus* in that its incipient hypocone arises from the basal cingulum instead of from the postprotocingulum, the difference being the initiation of the subfamily characteristics of the Adapinae and Notharctinae respectively. It would seem therefore that by Abbey Wood times some faunal differentiation, if not also isolation of the two areas, had already taken place. This reduces the reliance one might otherwise place on evolutionary grade in correlating Sparnacian and early Wasatchian faunas. Conversely, any significant time separation of the two faunas would be expected to have produced individual specializations in *H. wardi* as they have in *H. orientalis*. None are apparent in the material at present available, tending to support the correlation suggested above.

Hyopsodus is the second most abundantly represented element in the mammal fauna at Abbey Wood. It is surpassed only by *Hyracotherium*, which may reflect a collecting bias caused by past coarse-sieving methods. These were also the two most commonly found genera in the early Wasatchian mammal fauna of Powder River, Wyoming (Delson 1971 : table 1).

The tooth identified tentatively by Teilhard de Chardin & Fraipont (1921) as *Hyopsodus* from the Eocene fissure filling of Vinalmont, Belgium, was dismissed without explanation by Gazin (1968 : 8). From the figure it appears definitely condylarthran, but differs from early Eocene *Hyopsodus* in the following ways. It is more robust; the talonid is higher relative to the trigonid; the paraconid is central instead of lingual; the cristid obliqua trends only slightly mesiolingually and meets the trigonid at a high level; the talonid notch is narrow and shallow; it is much larger.

Family **PERIPTYCHIDAE** Cope, 1882

Subfamily **ANISONCHINAE** Osborn & Earle, 1895

Genus ***LESSNESSINA*** nov.

TYPE SPECIES. *Lessnessina packmani* sp. nov.

DERIVATION OF NAME. After the type locality in the woods of Lessness Abbey. Feminine.

DIAGNOSIS. Small anisonchine (P^3–M^3 length 11·0 mm; other measurements in Table 2). P^3–M^3 protocones large and high and with mesial and distal concavities. P^{1-2} relatively large. P^{3-4} similar to one another, short and broad. Upper molars with low buccal cusps and without ectocingulum. M^{1-2} with well-spaced paracones and metacones; prominent mesostyles; protocones approximately in line with and not buccal to small subequal protostyles and hypocones. M^3 reduced.

Lessnessina packmani sp. nov.

(Figs 7, 15)

HOLOTYPE. Left maxilla with alveoli for canine and P^1 and complete P^3–M^3 (M 29632).

PARATYPES (3). Right P^4 (M 29756), right M^1 (MC 17) and right M^3 (M 29637).

DOUBTFULLY REFERRED SPECIMEN. Protoconal fragment of a right or left P^3 or P^4 (M 34648).

DERIVATION OF NAME. In memory of the late Mr A. R. G. Packman, who collected the excellent holotype.

TYPE HORIZON AND LOCALITY. Lessness Shell Bed, Abbey Wood Member, Blackheath Beds, Sparnacian, early Eocene; the sandpit, Abbey Wood, London Borough of Bexley (TQ 480786). Known from no other horizon or locality.

DIAGNOSIS. Only known species of the genus.

DESCRIPTION. *Dental formula.* $\frac{?}{?}\ \frac{1}{?\,1}\ \frac{4}{?\,4}\ \frac{3}{?\,3}$. Only P^2–M^3 are materially known. Two, more mesial single-rooted teeth are represented by alveoli on the holotype. The more distal of these is not separated from either P^2 or the more mesial alveolus by diastemata. It once contained a root which was slightly recurved and longer than either of those belonging to P^2. The crown would have been broader than and almost as long as that of P^2. The remnant distal half of the more mesial alveolus indicates a longer and slightly more recurved root than the first.

These alveoli are considered to have contained the canine and P^1, as there is no maxillary/premaxillary suture to indicate that the mesial one is for an incisor, and no interalveolar diastema (i.e. occluding space for a lower canine) to indicate that the distal one is for the upper canine. P^1 is normally small in anisonchines (Matthew 1937 : 145–160). Small size of this tooth in mammals is often a prelude to its loss and it could be argued that in a late anisonchine the distal alveolus is more likely to have housed the canine. However, as P^2 in *Lessnessina* is somewhat enlarged, it seems more logical to postulate a foward continuation of this trend to explain a large P^1.

State of preservation of the holotype. The specimen is well-preserved but shows evidence of water transport. The natural edges (i.e. those not broken in collecting) approximately follow the sutural edges of the maxilla, but the convex bone surfaces are slightly worn and the buccal edges

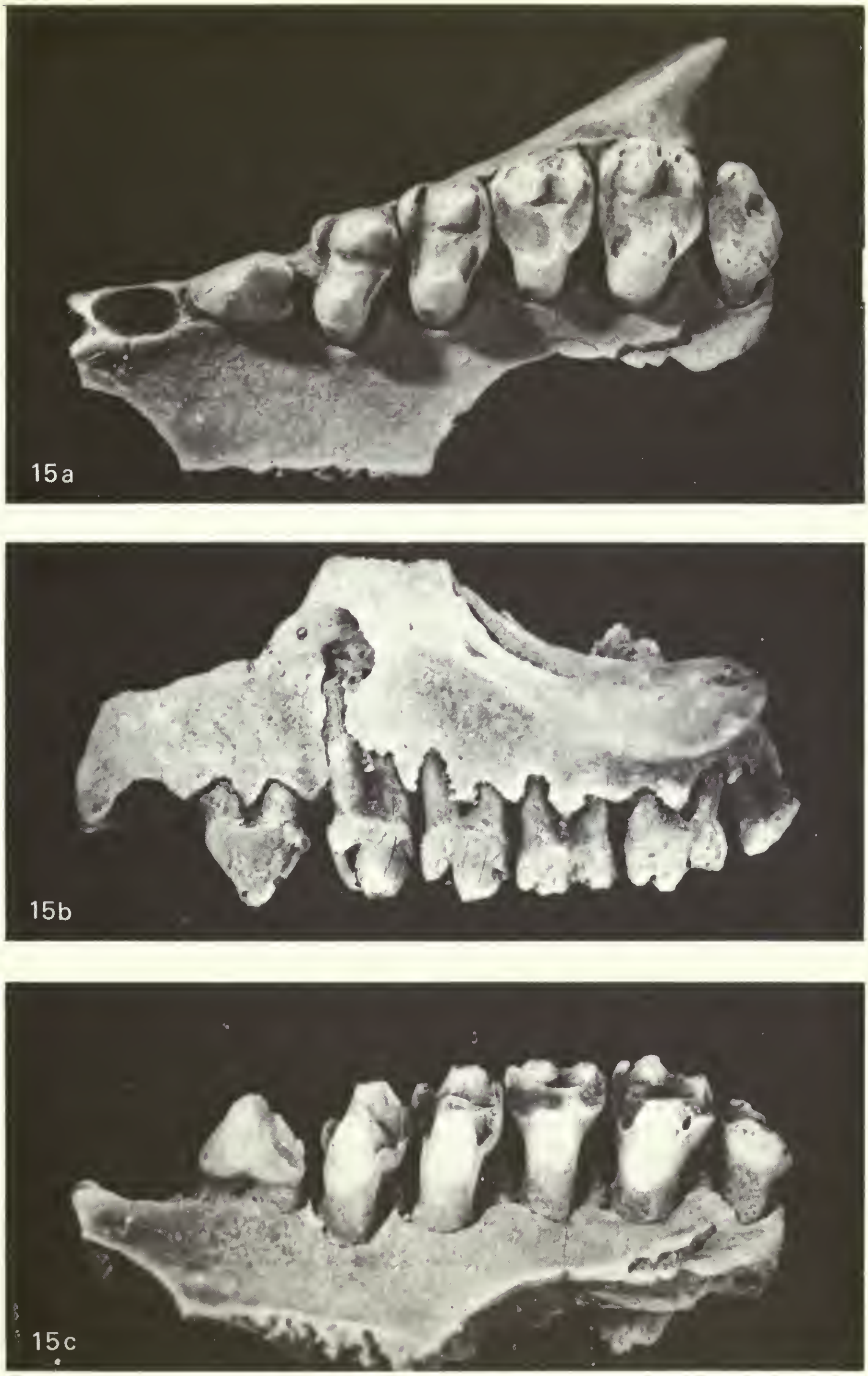

Fig. 15. *Lessnessina packmani* gen. et sp. nov. from the Blackheath Beds of Abbey Wood; **holotype** L maxilla with C and P^1 alveoli and P^2–M^3, M 29632; a, occlusal view; b, buccal view; c, lingual view. All views ×6 and sprayed with ammonium chloride.

of the teeth, particularly P^2, are somewhat abraded. Natural tooth wear is fairly advanced especially on M^1, indicating an old individual. P^4 is more worn than P^3, which is more worn than P^2. This could indicate either a mesially trending eruption sequence, perhaps in response to premolar enlargement in a mesial direction, or a relatively distal area for maximum mastication.

Upper dentition. Some of the tooth surfaces are slightly rugose. P^2 is long and narrow in outline, broader distally. It is dominated by the paracone. There are large distolingual and steep narrow mesial wear facets. It is separated from P^3 by a short diastema. P^3 is transversely elongated, with conical paracone and protocone. The parastyle is low but mesially salient. There are rather transverse pre- and postprotocristae, the latter being very weak. The long axis of the tooth is oblique so that the protocone is mesial to the paracone. P^4 is almost identical to P^3 but the parastyle is higher and extends more lingually; and the postprotocrista is stronger, joining the higher distal cingulum at a small cuspule. It is only slightly larger than P^3 in the holotype.

M^{1-2} are triangular in outline and transversely elongated. The lingual half shows a rather sudden narrowing where the large mesial and distal cingula terminate in small protostyle and hypocone. The mesostyle is linked to both paracone and metacone by a low, slightly buccally flexed centrocrista. Although on M^1 of both the holotype and MC 17 the paracone and metacone are worn to equal heights, the smaller area of exposed metacone dentine shows that this cusp was lower than the paracone, as can be seen more easily on the other two molars.

The most noticeable feature of the M^{1-2} and to a lesser extent of P^{3-4} and M^3 is the shallow convex lingual slope of the protocone whose enamel dives basally below the rest of the crown until it merges without overhang into the massive lingual root.

Wear on M^1 of the holotype is deep enough to have fused the protocone, paraconule, metaconule and the large mesial and distal cingula into one large area of dentine, with even a narrow dentinal isthmus extending from the paraconule region to the worn paracone tip. The holotype M^2 is less worn and the worn mesial cingulum stands isolated. The paraconule is still fused to the protocone but oddly the metaconule is independent of the protocone but fused to the distal cingulum. From the wear pattern of the holotype M^1 it is evident that this tooth also had its protocone and metaconule separated at an earlier wear stage. That this is a variable character is shown by MC 17 where the worn paraconule, protocone and metaconule are fused and independent of the cingula. The upper molar parastyles are strong but merge lingually with the mesial cingulum.

Table 2. Length and width measurements (mm to nearest 0·05) of *Lessnessina packmani* gen. et sp. nov.

Number	Tooth	l.	w.
M 29632 (ARGP) (holotype)	LP^1 alveolus	2·00	1·30
	LP^2	2·50	1·65
	LP^3	2·10	2·75
	LP^4	2·20	3·20
	LM^1	2·45	3·30
	LM^2	2·60	3·90
	LM^3	2·05	2·95
M 29756 (SAB)	RP^4	2·00	2·60
MC 17	RM^1	2·20	2·95
M 29637 (PRG)	RM^3	1·70	2·10

The holotype M^3 is rather worn and abraded and this tooth is best studied from the smaller paratype (M 29637). The tooth is triangular, tapering distally, with a terminal metacone. The paraconule and especially metaconule are poorly developed. Breakage on both specimens makes it difficult to decide whether or not there was a mesostyle. The distal cingulum curves at its lingual end up the side of the protocone.

Lower dentition. Although unknown, this would probably have been similar to that of *Hemithlaeus* except that M_{1-2} would have been relatively longer with more expanded talonids bearing large hypoconids; M_3 relatively smaller with reduced hypoconulid but larger hypoconid; P_{1-2} relatively large, P_2 a particularly tall tooth according to the long steep mesial wear facet of P^2.

Maxilla. The palatal process is preserved as far as the midline suture. Part of the lower half of the orbital floor remains and shows the maxillary canal beginning between P^4 and M^1 and emerging at the infraorbital foramen above the mesial half of P^3. The lower orbital margin was formed by the now missing jugal, its contact with the zygomatic process of the maxilla becoming a groove anteriorly. The fact that a portion of orbital rim composed of maxilla occurs anterodorsal to the jugomaxillary suture suggests that the lacrymal was confined to the orbit. The orbit appears to have extended anteriorly to above the junction of P^3 or P^4. A small elongated foramen occurs near the jugomaxillary suture at the level of P^4.

DISCUSSION OF RELATIONSHIPS. *Lessnessina*, the youngest anisonchine, extends the subfamily's upper stratigraphical limit from the Upper Palaeocene to the Lower Eocene and its geographical range from North America to Europe. *Androconus* Quinet, 1965, a supposed periptychid from the Oligocene of Hoogbutsel, Belgium, has been shown to be synonymous with the pantolestid insectivore *Cryptopithecus* Schlosser, 1890 (Heissig 1977).

Because of this considerable range extension, the relationships of *Lessnessina* require some justification. It has the following unspecialized condylarth features. Bunodont cusps, in combination with non-molariform distal premolars; small upper molar hypocones; upper cheek teeth with crowns passing basally into powerful roots without an overhanging lingual enamel edge; absence of M^{1-2} postprotocingulum. One or more of these distinguish it from superficially similar genera in the orders Insectivora such as *Paschatherium* and Primates such as *Plesiadapis*. From the primitive Artiodactyla such as *Diacodexis*, *Lessnessina* differs essentially in its reduced M^3 and short transverse P^3 as well as in some features which distinguish it also from hyopsodontid condylarths (see below).

Accepting its condylarthran affinities, one sees that the general style of dentition of *Lessnessina* is found only in the Hyopsodontidae and the anisonchine Periptychidae. It has been compared

Table 3. Comparative table of characters in *Lessnessina*, Anisonchinae (except *Lessnessina*) and Hyopsodontidae

Character	*Lessnessina*	Anisonchinae	Hyopsodontidae
P^3–M^3 length	11 mm	16–27 mm	10–28 mm
Nature of cusps	Bunodont	Bunodont	Semibunodont, crests usually more prominent
P^3 outline	Short, broad, resembling P^4	Short, broad, resembling P^4 in *Hemithlaeus* and *Anisonchus*	Triangular, unlike P^4 where known
Upper molar buccal cusps	Low	High	Low
Acute lingual tapering of upper molar outline with enamel extending basolingually	Yes	Yes	No
Relative size of M^1 metacone	Smaller than paracone	Smaller than paracone	Equal to paracone
Relative size of M^3	Reduced	Nearly as large as M^2	Reduced
Facial extension of lacrymal	Probably none	Little or none in *Haploconus* (*fide* Matthew 1937 : 159)	Large in *Hyopsodus*

with original specimens, casts or published figures of the genera contained in these groups, where the upper dentition is known. They comprise the Anisonchinae *Hemithlaeus*, *Conacodon*, *Anisonchus* and *Haploconus* (I follow Van Valen (1967) in referring *Coriphagus* to the Pentacodontidae), and the Hyopsodontidae *Choeroclaenus*, *Mioclaenus*, *Dracoclaenus*, *Protoselene*, *Promioclaenus*, *Ellipsodon*, *Jepsenia*, *Litaletes*, *Hyopsodus*, *Haplomylus*, *Phenacodaptes*, *Apheliscus*, *Aletodon*, *Paratricuspiodon*, *Tricuspiodon*, *Louisina* and *Microhyus* (I follow Van Valen (1967) in referring *Paschatherium* and *Litolestes* to the Adapisoricidae, to which I also tentatively add *Haplaletes* and *Litomylus*).

Table 3 compares key characters of *Lessnessina* with the rest of the Anisonchinae and the Hyopsodontidae. Similarities with the Anisonchinae predominate, particularly the important features of P^3 shape, the basolingual enamel extension of the upper molars and the ? non-facial lacrymal. Similarities to the Hyopsodontidae are restricted to rather more generalized characters.

ANCESTRY. Among the known Palaeocene anisonchines, *Lessnessina* is most like the structurally primitive *Hemithlaeus* from the Puercan (early Palaeocene) of New Mexico. *Hemithlaeus* P^{3-4} are, however, somewhat inflated and the parastyles are reduced. *Lessnessina* P^{3-4} are thus more like P^4 of the Puercan *Conacodon cophater* (Cope, 1884), but here P^3 has lost its protocone. Fundamental morphological similarity is thus closest to a hypothetical latest Cretaceous or earliest Palaeocene common ancestor of *Hemithlaeus* and *Conacodon*, where the premolars have not become inflated, P^3 has a protocone and the M^{1-3} hypocones have not enlarged. The evolution of *Lessnessina* from this stage would have involved:

1. ? reduction in overall size
2. reduction of M^3
3. enlargement of P^{1-2}
4. enlargement of P^3–M^3 protocones
5. ? expansion of M_{1-2} talonids with enlargement of hypoconids (hypothetical)
6. relative lengthening of upper and probably lower molars
7. acquisition of upper molar mesostyles.

This sequence of events is theoretical as there is no known genus which could be the immediate ancestor of *Lessnessina*. There is a gap of at least 10 million years between the latter and the probable time of its latest common ancestry with the other known anisonchines. The latter all appear to be too specialized to have given rise directly to *Lessnessina*.

Since this paper was submitted I have received from the American Museum of Natural History, through the courtesy of Mr E. Manning, casts of lower dentitions of the hyopsodontid *Oxyacodon*. They are quite dissimilar in detail from those of other hyopsodontids, especially in the structure of the lower molars. The distinct median paraconids (especially M_{2-3}), high trigonids and low talonids, prominent entocristids extending to tips of entoconids and metaconids, and mesiolingual cingula, all favour inclusion in the Anisonchinae. *Oxyacodon* lower molar talonids are relatively broader than in other anisonchines, but otherwise cusp pattern is rather similar to that of *Hemithlaeus*. This character is postulated above for the unknown *Lessnessina* lower molars. The reduced *Oxyacodon* P_{3-4} talonids also conform to the morphology expected for *Lessnessina* P_{3-4}, from the latter's simple P^{3-4}. For a related example, where uppers and lowers are known, compare the occlusal relationships of *Phenacodaptes* $P\frac{4}{4}$. It is possible, therefore, that *Lessnessina* is closer to *Oxyacodon* than to the other anisonchines. *O. agapetillus* (Cope) in particular extends the size range of anisonchines downwards almost to encompass *Lessnessina*.

Acknowledgements

I would like to thank the collectors and Dr D. E. Russell for making specimens available, Dr P. D. Gingerich for information and for providing casts of important specimens, staff of the Photographic Unit of the British Museum (Natural History) for the photographic illustrations, Mr J. Brydon and Dr R. P. S. Jefferies for Russian translation, and Drs A. W. Gentry, W. R. Hamilton and K. A. Kermack for critically reading the manuscript.

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Miocene sharks' teeth from Ecuador

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Synopsis

The first Miocene sharks from Ecuador are described. Representatives of nine genera are identified: *Procarcharodon*, *Odontaspis*, *Hemipristis*, *Galeocerdo*, *Negaprion*, *Carcharhinus*, *Scoliodon*, *Isistius* and *Aetobatus*. The shark fauna is comparable with those from the Miocene of other South American countries, the Caribbean, North America and Europe. The first occurrence of *Isistius triangulus* (Probst) in the Miocene of the western hemisphere is noted.

Introduction

During the years 1974–75, geologists from the Institute of Geological Sciences (Overseas Division) and the British Museum (Natural History) collected from the Neogene of Ecuador. Among the collections obtained were many sharks' teeth, which represent their first record from the Ecuadorian Miocene, and hence are of considerable interest. The teeth were collected by Drs C. R. Bristow and J. E. P. Whittaker. All but one of the teeth come from three localities CRB 123, a, b (Fig. 1), which occur along a 4 km stretch of coast just south of Bahia. One further tooth was collected from locality J 2a about 50 km north of Bahia. This tooth is included because of probable correlation with the beds from which the remainder were collected. The details of the localities are as follows. CRB 123 is a sea stack at Punta la Colorada, grid reference 602308, at 0° 37·6′ S, 80° 27·6′ W. CRB 123a is the cliff near the lighthouse at Punta Bellaca, grid reference 615330, at 0° 36·4′ S, 80° 27′ W. CRB 123b is the cliff at Punta la Gorda, grid reference 596298, at 0° 38·2′ S, 80° 28′ W. Grid references refer to the Cartographia Censal CC-MIII-D3 (123) Bahia de Caraquez, 1 : 50 000 map. Locality J 2a is at 0° 12′ S, 80° 20′ W.

A full description of the stratigraphy of this coastal area was published by Bristow (1976). He originally included the sharks' teeth from localities CRB 123, a, b in his faunal list for the Borbon Formation. Further work has shown, however, that the beds containing the teeth are transitional between the Onzole Formation and the overlying Borbon Formation. Here Borbon-type sandstones sometimes occur in Onzole-type blue silts and *vice versa* and it is difficult to refer the teeth to either of these Formations with certainty. Planktonic foraminifera from nearby sample CRB 124 (grid reference 609318) have dated these transitional beds as Zone N17 of Blow (1969), late Miocene (J. E. P. Whittaker, personal communication). Age-diagnostic species are *Sphaeroidinellopsis paenedehiscens* Blow, *Globorotalia plesiotumida* Blow & Banner and *Globorotalia humerosa* Takayanagi & Saito. The sample J 2a is from a part of the so-called Jama Formation which is thought to be equivalent to the Borbon Formation and also late Miocene.

The matrix is a medium-grained sandstone which has been recemented by weathering, especially at locality CRB 123, the sea stack from which the teeth were partly eroded out. This means that it is extremely hard and is difficult to remove without breaking the specimens. It tends to adhere more strongly to the roots, thus allowing only the crowns to become visible. Consequently many specimens consist of crown only.

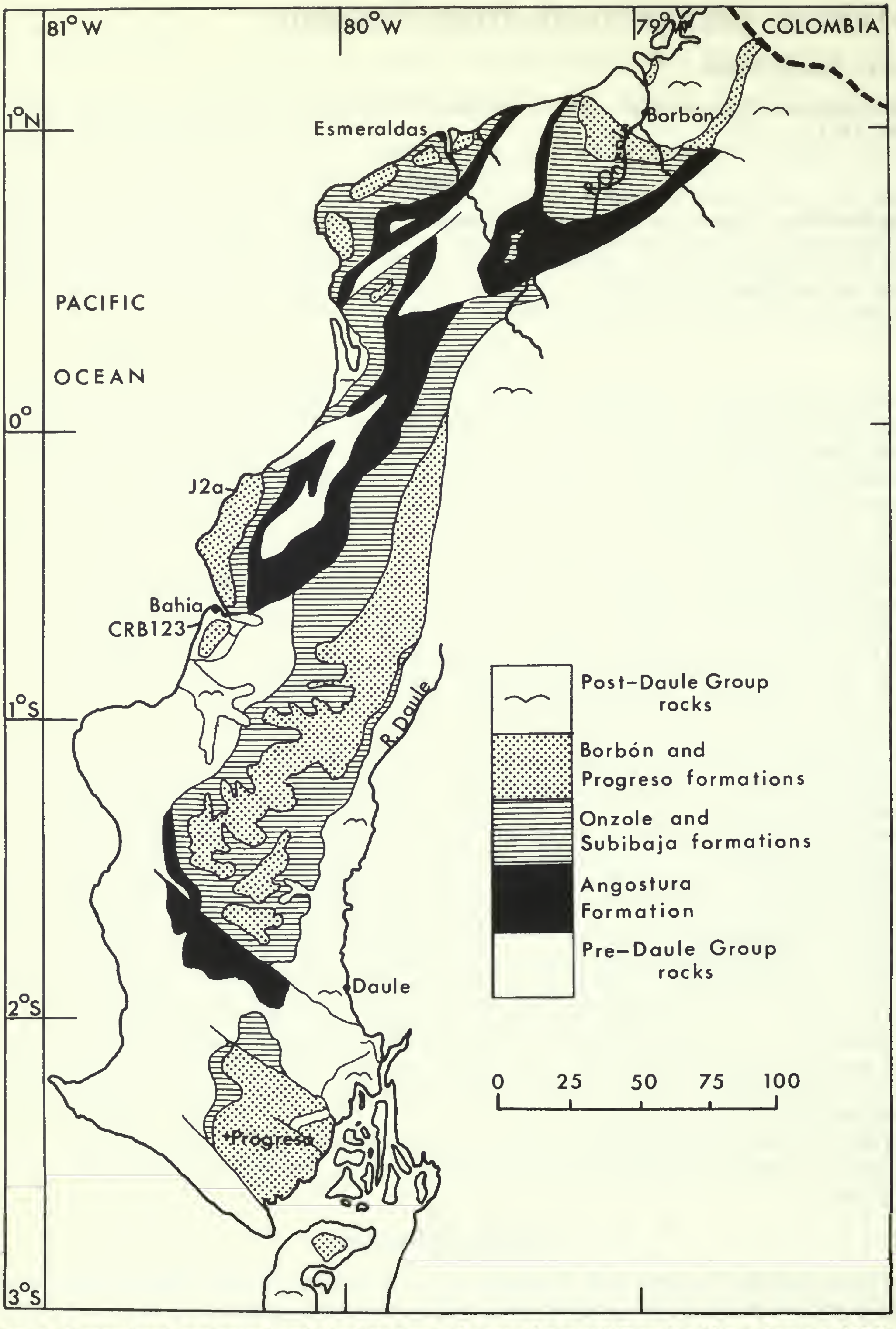
The teeth described are all now deposited in the collections of the British Museum (Natural History), London, and are referred to in this paper by the register number of that institution with a 'P' prefix.

Faunal Description

The fauna includes 9 genera, with 10 species, all in the subclass Selachii. Measurements quoted are the vertical height of the complete tooth, unless otherwise stated.

Bull. Br. Mus. nat. Hist. (Geol.) **32** (1) : 57–70.

Issued 28 June 1979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OCEAN
J2a
Bahia
CRB123
R. Daule
Daule
Progreso
Post-Daule Group rocks
Borbón and Progreso formations
Onzole and Subibaja formations
Angostura Formation
Pre-Daule Group rocks
0
25
50
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Fig. 1. Generalized geological and locality map of part of coastal Ecuador (from Bristow 1976); CRB 123 and J 2a are C. R. Bristow sample locality numbers.

Class **CHONDRICHTHYES**

Subclass **SELACHII**

Family **ISURIDAE**

Genus ***PROCARCHARODON*** Casier
Procarcharodon megalodon (Agassiz)

Synonymy. See Cappetta (1970).

Material. Four incomplete specimens, P.59278–81.

Localities. Three from CRB 123, one from CRB 123b.

Description (Fig. 2). The teeth are all fairly large (estimated height 8–9 cm) and typical of this species.

Family **ODONTASPIDAE**

Genus ***ODONTASPIS*** Agassiz
Odontaspis acutissima Agassiz

Synonymy. See Cappetta (1970).

Material. Eleven teeth, P.59265–74.

Localities. Nine from CRB 123, two from CRB 123b.

Description (Figs 3, 4). The teeth are typical of this species. Most of them lack a root and denticles, but they all have vertical striations on the inner face of the crown. Most appear to be anterior teeth.

Family **CARCHARHINIDAE**

Genus ***HEMIPRISTIS*** Agassiz
Hemipristis serra Agassiz

Synonymy. See Cappetta (1970).

Material. Two specimens, P.59275–6.

Locality. Both from CRB 123.

Description. One specimen consists of the root only and the other is the apex of a crown.

Genus ***GALEOCERDO*** Müller & Henle
Galeocerdo aduncus Agassiz

Synonymy. See Cappetta (1970).

Material. One tooth, P.59277.

Locality. CRB 123.

Description. This specimen is an almost complete tooth, still partly embedded in the matrix. The tooth is large, being 2·3 cm across the widest part at the base of the crown. The tip of the crown is missing so the height cannot be measured.

Genus ***NEGAPRION*** Whitley

Isolated teeth of this genus are difficult to distinguish from the lower teeth of some species of *Carcharhinus*. From descriptions of fossil and Recent (Bigelow & Schroeder 1948) examples of this genus some of the specimens in this collection are included in the genus *Negaprion*. All the specimens are here identified as *N. eurybathrodon* (Blake).

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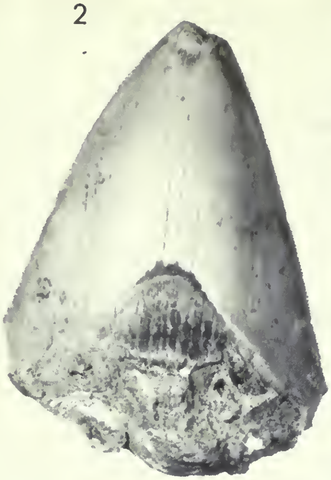

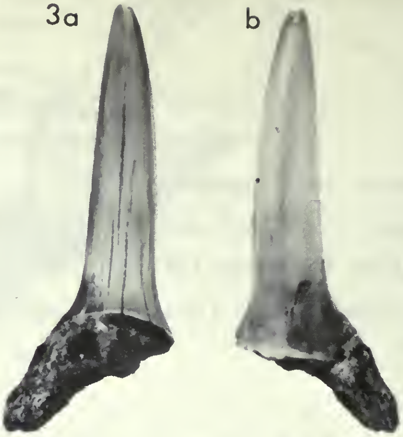

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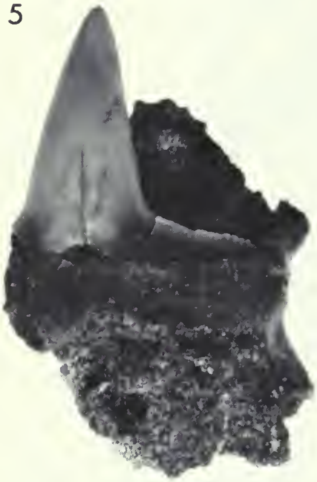

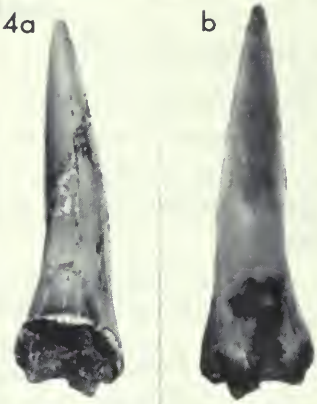

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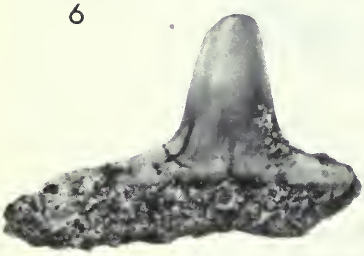


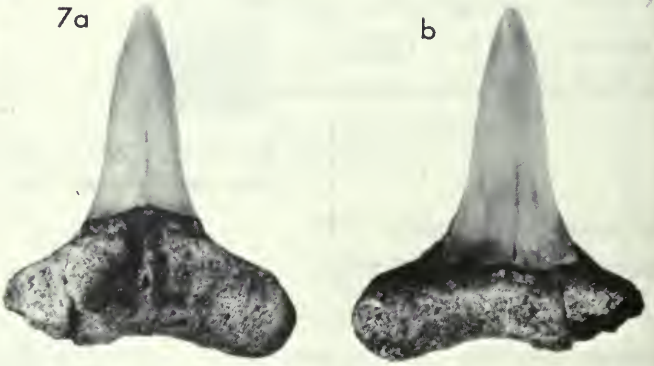


Fig. 2. *Procarcharodon megalodon.* P.59280, CRB 123, inner view, ×0·7.

Figs 3–4. *Odontaspis acutissima*, both CRB 123. (3) P.59267. (4) P.59266. (a) inner views; (b) outer views. ×2.

Figs 5–7. *Negaprion eurybathrodon.* (5) P.59262, CRB 123, outer view, ×2·2. (6) P.59263, CRB 123a, outer view, ×2·9. (7) P.59257, CRB 123 : (a) inner view; (b) outer view; ×2·4.

Negaprion eurybathrodon (Blake)

Synonymy. See Cappetta (1970).

Material. Nine teeth, P.59257–64.

Localities. One from CRB 123a, seven from CRB 123, one from CRB 123b.

Description (Figs 5–7). Some of the teeth are fairly complete, others incomplete or still partly embedded in matrix. Two of the larger teeth (heights 1·7 and 2 cm) appear to be upper teeth by White's (1955) description. These have more triangular crowns than the lower teeth, and flatter outer faces. They have a small central depression in the base of the enamel of the outer face. The lateral extensions of enamel along the roots have wavy edges. These two teeth are slightly asymmetrical and are probably lateral in position, since they also have wide roots.

The lower teeth are symmetrical, even those most lateral ones with wide roots. The lateral extensions of the enamel, when visible, show only slight crinkling along the edges in some specimens. The teeth have a convex inner face and a bulbous outer face to the crown, especially at the base of the enamel. It is this character, and the lack of serrations on the main part of the crown, that distinguishes these teeth from the lower teeth of the *Carcharhinus* species in this fauna.

Genus *CARCHARHINUS* Blainville

This genus contains many living species with a variety of tooth types. The upper teeth tend to have triangular crowns with fine regular serrations along the edges. The lower teeth have narrower upright crowns with or without serrations, depending on the species. The unserrated lower teeth of some species are difficult to distinguish from those of species in other genera (e.g. *Negaprion*, *Hypoprion*) and other anatomical details are used in identifying Recent species, since teeth alone are not reliable. Fossil teeth of the unserrated type can therefore only be arbitrarily attributed to a genus and species, as with the foregoing *Negaprion*. The same is true when trying to associate upper and lower teeth as one species. I have placed two of the following types of teeth into one species, *C. egertoni*, because of custom, and because they fit the accepted descriptions of this species in Leriche (1942).

Carcharhinus egertoni (Agassiz)

Synonymy. See Antunes & Jonet (1969).

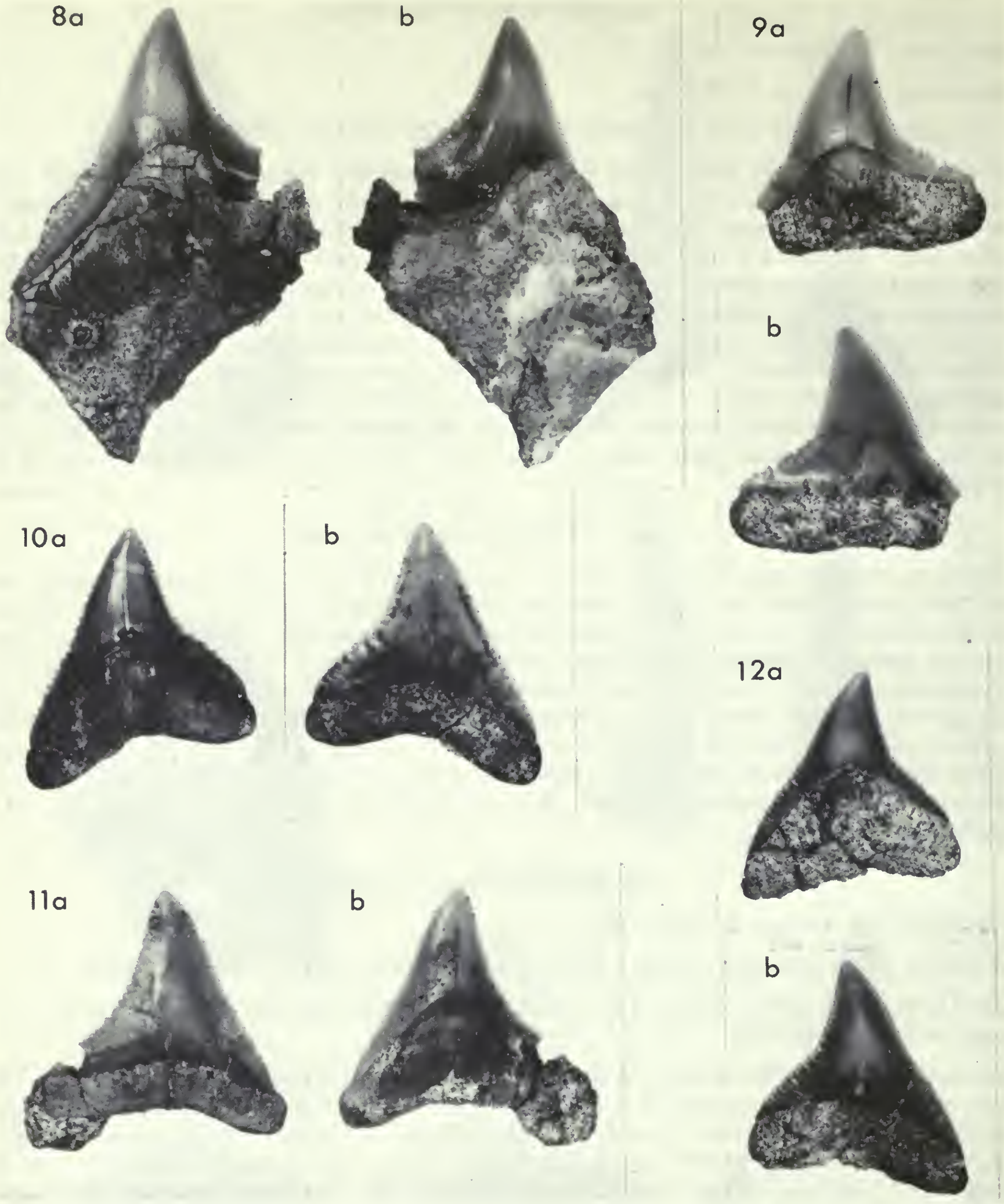
Material. Forty-nine upper teeth, P.59215–236, P.59244–6. Six lower teeth, P.59237–42.

Localities. Upper teeth, 43 from CRB 123, two from CRB 123a, four from CRB 123b. Lower teeth, six from CRB 123b.

Description (Figs 8–19). Most of the upper teeth lack roots or are embedded in the matrix. They have broadly triangular crowns on a wide root. The crowns all show strong regular serrations, which become slightly coarser towards the base. The heights of the crowns vary from 7·3 mm to 15 mm, and within the sample there is a continuous size range. Anterior and lateral teeth are present, with the crowns becoming more asymmetrical and the roots becoming wider in the lateral teeth. There are crenulations at the base of the enamel on the outer face of the larger teeth. Many teeth have a central, raised pad of enamel at the base of the outer face.

In these teeth the roots are narrower and the serrations finer than those of *Carcharhinus priscus*. The crowns also tend to be more triangular. The central pad of enamel is not present in *C. priscus*. The majority of the teeth are larger than described examples of *C. priscus*.

The lower teeth are much fewer and are restricted to one locality. They have slender crowns which are symmetrical. All the specimens collected have narrow roots. The outer faces are more convex than those of the upper teeth. The crowns bear serrations at the tip only and when viewed from the outer side the crowns expand at the serrated part. In most the cutting edge is only strongly developed at the tip and is not very clear on the lower half of the crown. This is not due to wear since the fine serrations are still visible at the tip.

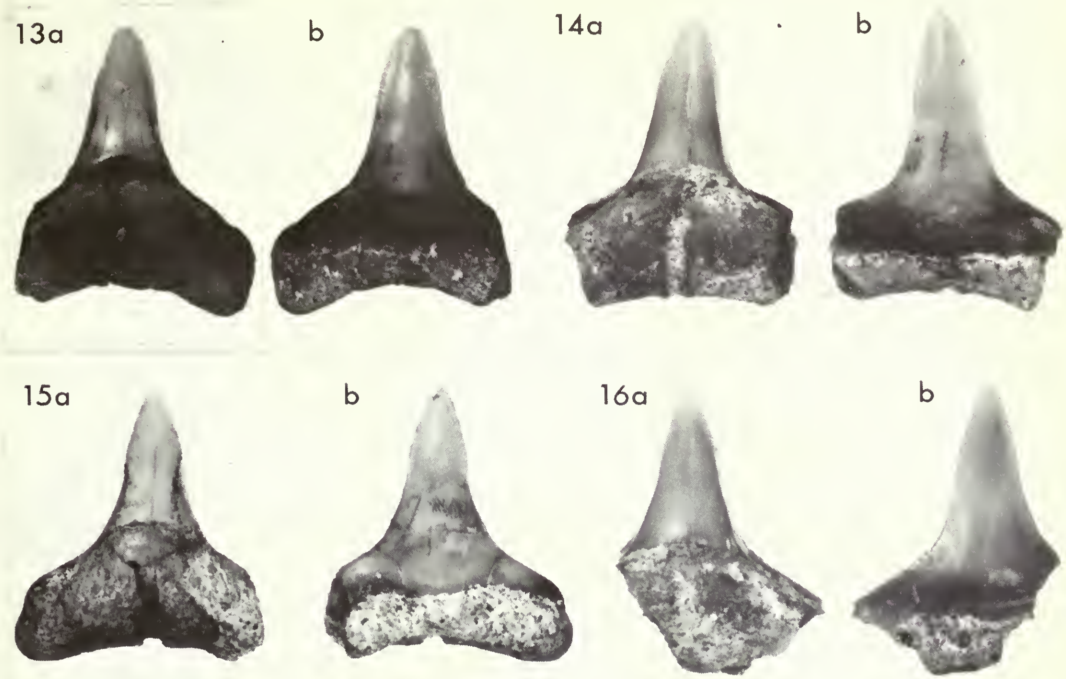


Figs 8–12. *Carcharhinus egertoni*, upper teeth, all CRB 123. (8) P.59215. (9) P.59225. (10) P.59217. (11) P.59216. (12) P.59219. (a) inner views; (b) outer views. All approx. ×2.

These teeth fit the description of *C. egertoni* by Leriche (1942 : fig. 6). As White (1955) says, there does not seem to be much difference between this species and the Recent *Carcharhinus longimanus* (Poey), the lower teeth being very similar.

The difference in the numbers of upper and lower teeth may be an effect of preservation or collection. However, there is a possibility that the upper teeth represent more than one species. Two of the smaller ones show some similarity to *C. priscus* in having narrower crowns and coarser serrations.

Three of the upper teeth (Figs 17–19) show some variation. The crowns lean distally. The distal edge is concave and the mesial edge convex, especially so about half-way up the crown. This pronounced convexity is not present in the other specimens. Leriche (1942 : pl. 8, fig. 4) and Eastman (1904 : fig. 1) figure teeth similar to these as *C. egertoni.*



Figs 13–16. *Carcharhinus egertoni*, lower teeth, all CRB 123b. (13) P.59237, ×3. (14) P.59238, ×3. (15) P.59239, ×2·5. (16) P.59240, ×3. (a) inner views; (b) outer views.

Carcharhinus cf. ***priscus*** (Agassiz)

Synonymy. See Cappetta (1970).

Material. Seven ? lower teeth, P.59247–53.

Localities. Six from CRB 123, one from CRB 123b.

Description (Figs 23–24). The teeth all have slender crowns on wide bases. The crowns are upright or incline slightly distally. These teeth also have fine serrations along the whole edge of the crown. They are very similar to the following species but are much smaller.

These teeth are like those of *C. priscus* shown in Cappetta (1970 : pl. 14, figs 1–20) and examples in the British Museum (Natural History) from Montpellier and Florida. However, they have more definite serrations and the roots are separated by a more acute angle. The crowns are also narrower.

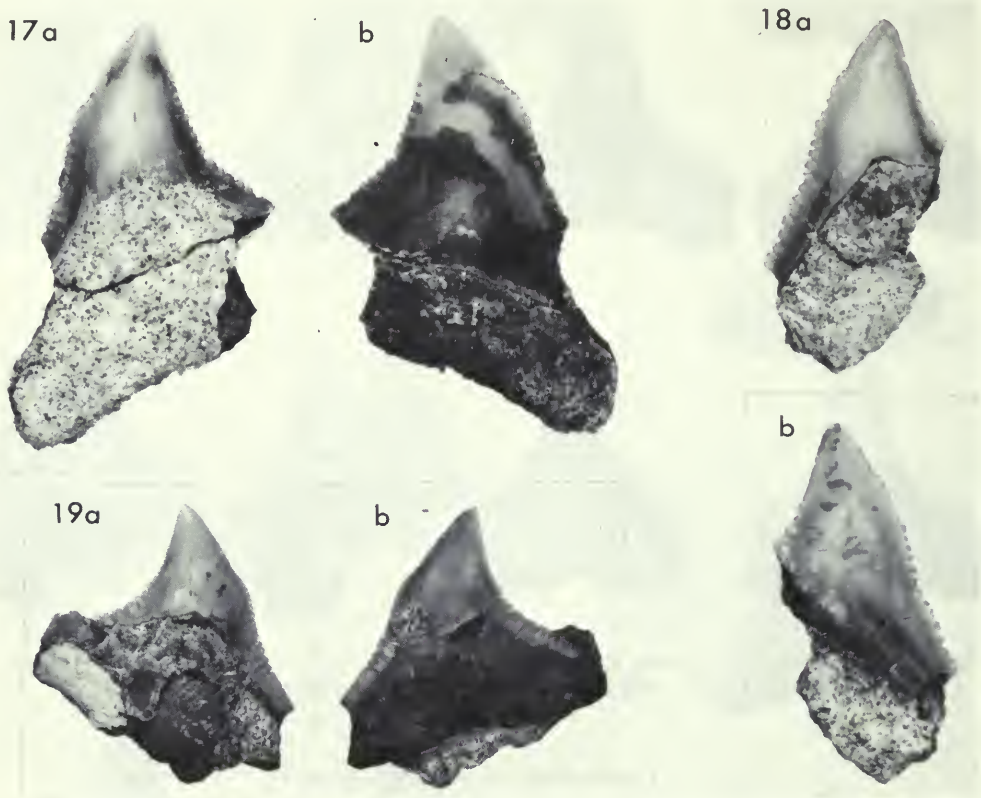
Carcharhinus sp.

Material. Three ? lower teeth, P.59254–6.

Localities. Two from CRB 123, one from J 2a.

Description (Figs 20–22). The teeth have symmetrical crowns on wide bases. The crowns are narrower than those of the upper teeth of *C. egertoni.* The outer face is slightly convex, the inner more so. These teeth have fine regular serrations along the whole edge of the crown and along the basal lateral extensions of enamel, and so differ from the lower teeth of *C. egertoni.* The teeth are fairly large and measure 1·6 cm, 1·49 cm and 1·35 cm in height.

The teeth are similar to upper teeth of *C. priscus*, but differ in their larger size and finer crenulations. These crenulations do not become coarser towards the base as they do in *C. priscus* and *C. egertoni.*



Figs 17–19. *Carcharhinus egertoni*, upper teeth, all CRB 123. (17) **P.**59244, ×2·9. (18) **P.**59245, ×2·6. (19) **P.**59246, ×1·8. (a) inner views; (b) outer views.

Genus *SCOLIODON* Müller & Henle
Scoliodon taxandriae Leriche

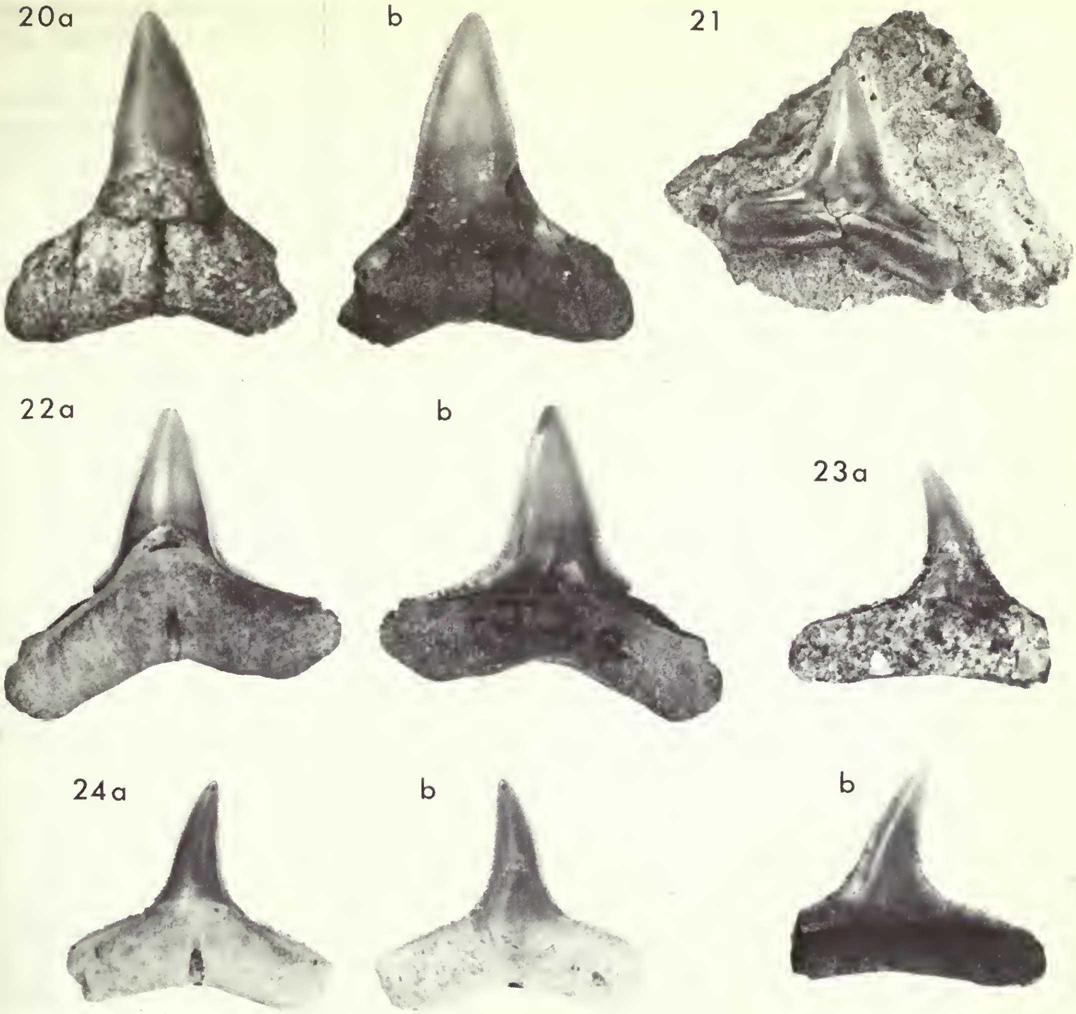
SYNONYMY. See Antunes & Jonet (1969).

MATERIAL. Four teeth, P.59285–8.

LOCALITY. CRB 123b.

DESCRIPTION. Two of the teeth (P.59285–6) have triangular crowns which are inclined distally. The mesial edge is a continuous concavity, the distal edge is more or less vertical and has a notch where it joins the distal denticle. The distal denticle has a slightly wavy edge. The inner and outer faces are convex, with the enamel on the outer face ending basally in a horizontal pad. A distinctive oblique nutritive groove on the inner face also produces a notch visible, from the outer side, between the roots.

The two other teeth are about the same size as the previous two (5·5 mm and 3·7 mm high). They are similar to the above teeth except that the mesial edge is less concave and the outer



Figs 20–22. *Carcharhinus* sp. (20) P.59254, CRB 123; (a) inner view; (b) outer view; ×2·9. (21) P.59255, CRB 123, outer view; ×2. (22) P.59256, J 2a, (a) inner view; (b) outer view; ×2·3.
Figs 23–24. *Carcharhinus priscus.* (23) P.59247, CRB 123, ×3·8. (24) P.59253, CRB 123b, ×3·5. (a) inner views; (b) outer views.

face is flat. Instead of a horizontal pad at the base of the outer face, there is a medial triangular depression in the enamel.

Family SCYMNORHINIDAE

Genus *ISISTIUS* Gill
Isistius triangulus (Probst)

Synonymy. See Cappetta (1970).

Material. Three lower teeth, P.59282–4.

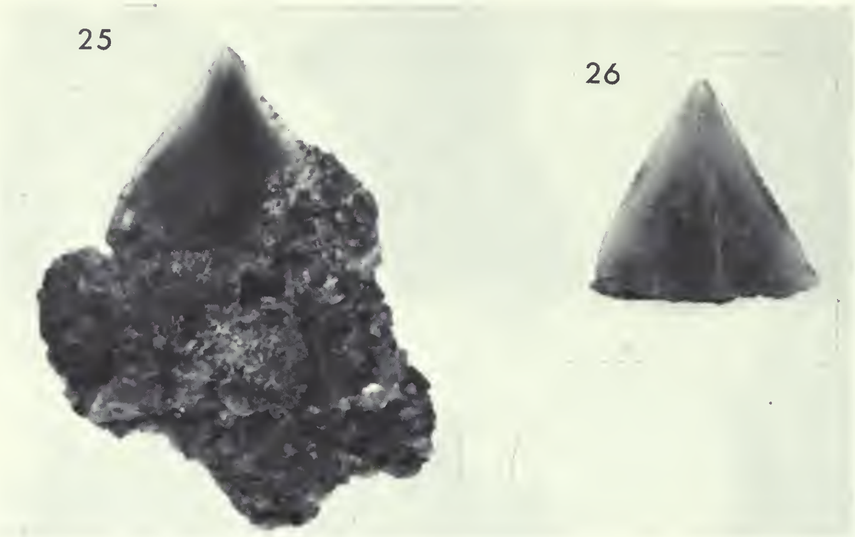
Localities. Two from CRB 123, one from CRB 123a.

Description (Figs 25–26). Two of the specimens are still partly embedded in matrix. One of these shows half the root with an indication of the central foramen (Fig. 25). The other two specimens are crowns only. One specimen shows an indication of crenulations along the edge. All three crowns are triangular, very thin and typical of this species. They are all anterior teeth and fairly large for this species, with crown heights of 4·5 mm.

This is the first definite record of *Isistus triangulus* in the Miocene of the western hemisphere. Casier (1958) described specimens of *Isistius* sp. from Barbados. In 1966 he redescribed them as *Sphyraena kugleri* Casier and figured more examples. However, his pl. 3, fig. 27 appears to be a specimen of *Isistius triangulus* and is thus included in Table 1.

Family **MYLIOBATIDAE**

A few teeth of *Aetobatus* sp. and possibly *Myliobatis* sp. are present in the fauna but these are very worn or still embedded in the matrix and are not identifiable to species.



Figs 25–26. *Isistius triangulus*, lower teeth. (25) P.59284, CRB 123a, inner view. (26) P.59282, CRB 123, outer view. Both ×6·6.

Discussion

This is the first fauna of sharks to be described from the Miocene of Ecuador. The Miocene deposits along the coast of Ecuador are up to 5000 ft (1520 m) thick (Sheppard 1928) and much work has been done on the foraminifera and mollusca of these deposits. References to Miocene sharks from South America are sparse. Table 1 is a summary of the known geographical distribution of the species in this fauna. I know of no references to sharks' teeth from the Miocene of Colombia. Small faunas from Chile (Oliver-Schneider 1936, 1937), Peru (Hoffstetter 1968) and Venezuela (Leriche 1938, Rodríguez 1968) contain little more than the cosmopolitan *Procarcharodon megalodon*. The Peruvian fauna is thought to be uppermost Miocene like the one from Ecuador. Leriche (1938) says that *Hemipristis serra* and *P. megalodon* from Venezuela are also from the Upper Miocene. The other faunas are merely stated as being from the Miocene.

Of the other South American countries, a large fauna is described from the Pirabas Formation of Brazil (Santos & Travassos 1960, Santos & Salgado 1971). This fauna is Lower Miocene in age, older than the Ecuador fauna, but five species are common to both faunas. The Brazilian fauna includes *Scoliodon taxandriae*, and this is the only other record of this species from the western hemisphere.

Records of the Argentinian Miocene faunas are controversial. Sharks' teeth from the Patagonian and Paraná formations have been described. Leriche (1907) described sharks from the

Table 1. The geographical distribution of the species

	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17	18	19	20	21	22	23	24	25	26	27	28	29	30	31	32	33	34
Procarcharodon megalodon	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+
Odontaspis acutissima	+			+				+	+				+			+		ø[1]					+	+	+	+	+	+	+	+	+	+	+	+
Hemipristis serra	+			+	+	+	+	+	+			+	+	+	+	+	+	+	+	+	+		+	+	+	+	+	+	+	+		+	+	+
Galeocerdo aduncus	+			+					+				+		+	+	+	+	+	+	+		+	+	+	+	+	+	+	+	+	+	+	+
Negaprion eurybathrodon	+													+		+	+			+						+								+
Carcharhinus egertoni	+		+	+		+	+	+								+	+	+	+	+						+							+	
Carcharhinus priscus	+		+	+		+									ø	+					ø		+	+	+	+	+	+	+	+	+	+	+	
Carcharhinus sp.	+																																	
Scoliodon taxandriae	+					+																	+			+					+			
Isistius triangulus	+							+															+			+		+		+				
Aetobatus arcuatus[2]					+										ø	+	+		+		ø		+	+	+	+		+	+	+		+		

South America

1 Ecuador
2 Chile (Oliver-Schneider 1936)
3 Peru (Hoffstetter 1968)
4 Argentina (Leriche 1907, Woodward 1900, Ameghino 1906, Pascual & Rivas 1971)
5 Venezuela (Leriche 1938, Rodríguez 1968)
6 Brazil (Santos & Travassos 1960, Santos & Salgado 1971)

Caribbean

7 Trinidad (Leriche 1938, Casier 1958)
8 Barbados (Leriche 1938, Casier 1958, 1966)
9 Cuba (Leriche 1938, Kruckow 1957)
10 Jamaica (Leriche 1938)
11 Haiti (Leriche 1938)
12 Mexico (Leriche 1938, Kruckow 1959)
13 Baja California (Kruckow 1957)
14 Panama (Leriche 1938, White 1955)

North America

15 California (Leriche 1942)
16 Maryland (Leriche 1942, Eastman 1904)
17 North Carolina (Leriche 1942)
18 South Carolina (Leriche 1942)
19 Virginia (Leriche 1942)
20 New Jersey (Leriche 1942)
21 Florida (Leriche 1942)
22 Mississippi (Leriche 1942)

Europe

23 Montpellier (Cappetta 1970)
24 East France (Cappetta 1970)
25 Italy (Cappetta 1970)
26 Portugal (Cappetta 1970, Antunes & Jonet 1969)
27 Spain (Cappetta 1970)
28 Switzerland (Cappetta 1970, Leriche 1927)
29 Austria (Cappetta 1970)
30 Germany (Cappetta 1970)
31 Belgium (Cappetta 1970)
32 Holland (Cappetta 1970)

33 *Africa* (Cappetta 1970, Dartevelle & Casier 1943)

34 *Australia* (Cappetta 1970, White 1955)

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[1] ø indicates specimens from this locality present in the British Museum (Natural History) collections, but not mentioned in the references.

[2] This species is included for comparison, since the *Aetobatus* specimens from Ecuador are not identified to species.

Patagonian and thought it might contain a mixture of Miocene (with *Isurus hastalis* (Agassiz), *Procarcharodon megalodon* and *Galeocerdo aduncus*) and Oligocene species (with *Odontaspis cuspidata* Agassiz and *Isurus desori* (Agassiz)). Priem (1911) thought the fish and cetaceans indicated an Early Miocene age for the Patagonian, whereas the molluscs indicated an Eocene/Cretaceous age. Ameghino (1889, 1906) described the Tertiaries of Argentina in great detail. He gave a list of sharks found in the Patagonian and said it was probably Early Eocene in age, despite the presence of Cretaceous species such as *Corax rothi* Ameghino, *Isurus angustidens* (Reuss) and *Scapanorhynchus subulatus* (Agassiz).

Ameghino also gave a faunal list for the Paraná group. This includes *Carcharhinus egertoni*, *Procarcharodon megalodon*, *Galeocerdo aduncus* and other typical Miocene species. He said they came from the marine Enterienne Formation of Paraná, and concluded the formation was Upper Oligocene in age. Woodward (1900) questioned this and because of the presence of the above sharks thought the Paraná was Upper Miocene or Lower Pliocene. More recently Pascual & Rivas (1971) have revised the vertebrate faunas of the Tertiary of Argentina. They give a shark faunal list, based on the works of Ameghino, for the marine facies of the Patagonian Formation and the 'Enterriense'. They arrive at a Lower Miocene age for the Patagonian, based on the cetacean and penguin faunas also found. Simpson (1972 : 6) agrees with this and says: 'Some marine beds confused with or even included in parts of the Patagonian Formation may be older, but it remains highly probable that the greater or typical part of the formation is not older than late Oligocene, more likely early Miocene, and that the same determination applies to the fossil penguins.' The shark fauna, as stated earlier, includes many Eocene and Cretaceous species.

Pascual & Rivas (1971) give faunal lists for the 'Enterriense', 'Mesopotamiense' and 'Rionegrense' of the Paraná. The shark determinations again are probably from Ameghino and include usual Miocene forms. The majority of other vertebrates listed, however, are terrestrial mammals and these indicate a Pliocene age for the Paraná. Pascual & Rivas say that there seems to be a mixture of terrestrial and marine faunas and they have included all the genera cited in previous works whether terrestrial or marine. They say that the rarer forms seem to be older and possibly represent secondarily derived fossils. They do not say whether they consider the sharks to be derived. This does seem possible in view of their probable Miocene age.

I have included *P. megalodon*, *O. acutissima*, *C. egertoni*, *C. priscus*, *H. serra* and *G. aduncus* in Table 1 as being probably from the Miocene of Argentina based on the above evidence.

The information for the Caribbean region is mostly from Leriche (1938); other references are given in Table 1. Most of the faunas are merely described as Miocene in age. Exceptions to this are the specimens of *N. eurybathrodon* from Panama, which are from the Middle Miocene (White 1955). Casier (1958) describes *H. serra*, *P. megalodon* and *C. egertoni* from the Lower Miocene of Trinidad, and *C. egertoni* and *H. serra* from the Upper Miocene. The Bissex Hill Formation of Barbados is Lower Miocene and considered to be contemporaneous with the Calvert Formation of Maryland (Casier 1958, 1966). *P. megalodon* and *H. serra* from Mexico are also from the Lower Miocene (Leriche 1938, Kruckow 1959).

The information for the North American faunas is taken from Leriche (1942) and Eastman (1904). The Maryland faunas have been studied by Eastman (1904), however the sharks' teeth all come from the Calvert Formation in the Lower Miocene. *Aetobatus arcuatus* is the only species recorded from the St Mary's Formation (Upper Miocene) by Eastman. Leriche (1942) says that a specimen of *Odontaspis acutissima* is also possibly from the Upper Miocene. The other American records in Leriche (1942) are Lower Miocene or undifferentiated Miocene. There are many more recent references to the Miocene of North America but it is not within the scope of this paper to review them all.

The European distributions are taken from Cappetta (1970) and Antunes & Jonet (1969). Cappetta gives a good comparison of these faunas, including Lower, Middle and Upper Miocene. Table 2 (taken from Cappetta (1970) and Antunes & Jonet (1969)) shows that all the Ecuadorian species range into the Upper Miocene in Europe. The faunas from Montpellier and Portugal correspond closely to that of Ecuador. The Montpellier fauna does not include *C. egertoni*, *N. eurybathrodon* and the *Carcharhinus* sp., but the first two are present in Portugal.

The Ecuadorian fauna is therefore typically Miocene and compares closely with those of

Table 2. Distribution of the species in the Oligocene and Miocene

	Olig. L	Olig. M	Olig. U	Mioc. L	Mioc. M	Mioc. U
Procarcharodon megalodon				I	—	I
Odontaspis acutissima	I	—	—	—	—	I
Hemipristis serra				I	—	I
Galeocerdo aduncus			I	—	—	I
Negaprion eurybathrodon				I	—	I
Carcharhinus egertoni				I	—	I
Carcharhinus priscus		I	—	—	—	I
Scoliodon taxandriae				I	—	I
Isistius triangulus					I	I
Aetobatus arcuatus				I	—	I

Montpellier and Portugal, both of which have been very well studied. It differs from the Montpellier fauna in the absence of small sharks' teeth of several species. Further collecting in Ecuador is necessary for the study of the shark-tooth microfauna.

Table 3 shows the bathymetric and climatic ranges of Recent members of the genera present in the Ecuador collection. The molluscan and foraminiferal faunas of the Miocene of Ecuador both indicate deposition in warm, fairly shallow water. This interpretation is supported by the shark fauna, which has a predominance of supposed near-shore littoral forms. The Recent species are also tropical to subtropical in range. *Isistius* is the only pelagic form, but this is also neritic in habit, and could range into shallower water.

This fauna from Ecuador is important for the confirmation of the presence of *Scoliodon taxandriae* and *Isistius triangulus* in the western hemisphere, and in the variety of *Carcharhinus* teeth present. Future collections from the Miocene deposits of Ecuador, and also Colombia, could prove useful in furthering the study of the genus *Carcharhinus* and in extending the known geographical range of other Miocene species.

Table 3. Bathymetric and climatic ranges of the genera

	littoral	pelag.	bathy.	trop.	sub-trop.	temp.
Carcharodon	=	+		=	+	
Odontaspis	×	=		=	+	=
Hemipristis	+			×	=	
Galeocerdo	+	+		+	×	=
Negaprion	×			×	=	
Carcharhinus	=	+		+	+	
Scoliodon	×	=		+	+	
Isistius		×	=	+	+	
Aetobatus	+			+		

× occurrence abundant + occurrence common = occurrence rare

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A new fossil terrestrial isopod with implications for the East African Miocene land form

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Synopsis

A new species of fossil terrestrial isopod *Eubelum rusingaense* sp. nov. is described from the Lower Miocene of Rusinga Island, Lake Victoria, Kenya. It is suggested that the animal lived at about 2500 m within the montane forest litter. The invalid family group names Atracheata and Pseudotracheata (Vandel 1960) are replaced by Oniscacea and Porcellionoidea.

Introduction

The British–Kenya Miocene Expedition of 1947 (Leakey 1953, Leakey & Clark, 1955) collected a large quantity of fossil material from Rusinga Island, Lake Victoria, Kenya. A selection of arthropod fossils from this area has been figured, but without description, by Leakey (1953*a* : 445). Amongst the 'myriapod' specimens deposited in the British Museum (Natural History), London, were 46 specimens of a pseudotracheate terrestrial isopod of the family Eubelidae. This is the first recorded occurrence of the family as a fossil. This family, with the Armadillidae and Armadillidiidae, represent the most highly evolved group of conglobating forms within the Oniscoidea. Forms described from an older horizon, the Eocene–Oligocene Baltic Amber, all belong to the more primitive families Oniscidae, Porcellionidae and Trichoniscidae. The Armadillidiidae represented by *Armadillidium molassicum* (Heer, 1865) is found in the Miocene of Oeningen. The family Eubelidae is now essentially a family with a tropical distribution. The sole exception is *Sphaerobathytropa ribauti* Verhoeff, found in the central Pyrenees, but Vandel (1943) considered this species to represent a pre-glacial remnant fauna.

Fossil terrestrial isopods are rarely found and the handful of species so far described hardly allows a phylogeny to be erected which is backed up by fossil evidence. Edney (1960), however, supposed that the marine isopods left the sea via the littoral in the middle Mesozoic, whilst Vandel (1943 : table 2) proposed that the terrestrial forms were developed from the marine Cirolanidae. The latter are well represented in the fossil record (Jurassic–Recent) if the genus *Palaega* is accepted within this family, as suggested by Rathbun (1935) and Imaizumi (1953). Considering the world-wide tropical distribution of the Eubelidae and especially their occurrence in the Americas, Africa and southern India, the latest date for the establishment of the family is Albian, since it was at about this time that the Guinea–Brazil areas became separated (Maack 1969). Edney (1954, 1968) and Warburg (1968) have dealt in detail with the morphological and behavioural adaptations required to survive on land.

Systematic description

Order **ISOPODA** Latreille, 1817

Suborder **ONISCOIDEA** Latreille, 1803

Superfamily **PORCELLIONOIDEA** Verhoeff, 1918
[*nom. transl.* Morris herein, *ex* Porcellionidae Verhoeff, 1918]
(=Pseudotracheata Vandel, 1960).

Vandel (1960 : 95) formalized the classification of the Oniscoidea. Unfortunately in the tribe Crinocheta the two family group names that he chose, Atracheata and Pseudotracheata, were not based on an included nominate genus and are therefore invalid names under the Rules

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(Art. 11(e)). The replacement name for the Atracheata must be Oniscacea [*nom. transl.* Morris herein, *ex* Oniscia Rafinesque-Schmaltz, 1815 : 101]. The new names are used in exactly the same sense as Vandel's (1960) replaced names and with the same included families.

Family **EUBELIDAE** Budde-Lund, 1899

Genus ***EUBELUM*** Budde-Lund, 1885

TYPE SPECIES. *Eubelum lubricum* Budde-Lund, 1885 by monotypy.

RANGE. Lower Miocene to Recent.

Eubelum rusingaense sp. nov.

(Figs 1-11)

DIAGNOSIS. *Eubelum* with three-jointed antennal flagellum. Eyes with 17–19 ommatidia. Profrons folded onto vertex. Triangular escutcheon present. Shallow groove on coxopodite ridge of first pereion segment. *Schisma* and *sulcus arcuatus* present. Telson not divisible into two parts. Uropod protopodite almost completely fills space between the fifth pleonite and telson. Distal part of telson converging posteriorly.

LOCALITY AND HORIZON. Clark & Leakey (1951 : 9) locality R.1a from between Hiwegi Hill and the east coast of Rusinga Island, Lake Victoria, Kenya. The beds are of Lower Hiwegi Series, Lower Miocene age.

HOLOTYPE. BM(NH) In.61025

PARATYPES. In.61026–In.61070.

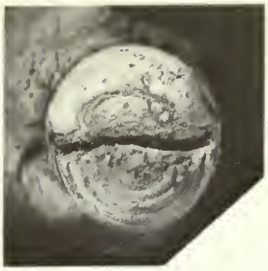
DESCRIPTION. Cephalon with convex protrons pushed up over the vertex and extending as a ridge along the frontal line. The frons is prominent with shallow lateral antennal grooves. Antennary tubercle raised into ridge; clypeus convex. There is a prominent median spine of the frontal lamina. Labrum strongly convex, rounded, triangular with the ventral portion bearing two strong laterally-directed ridges. A triangular escutcheon is developed. The mandibles are quadrate.

The anterior margin of the first pereion has a moderately sulcate margin and a straight posterior margin. The thickened coxopodite ridge of the epimeron of the first pereionite has a shallow ventrolateral groove. The epimeron is contiguous with the segment but the junction is marked by a deep *sulcus arcuatus* running parallel to and all the way along the lateral margin. A *schisma* is present and the internal lobe is the largest. The marginal edges of the second to fourth pereionites are rounded and thinned for their combined insertion into the *schisma* during enrollment. The fifth to seventh pereionite margins are squared off with a gentle lateral curvature. The pleonite segments are similarly squared off.

The telson is not divisible into two parts, having arcuate lateral margins and a gently rounded posterior margin. The uropod protopodite fills the space between the telson and the fifth pleonite. The body is capable of complete or nearly complete conglobation. There are sparse minute pits on the thoracic segments especially along the posterior bands of the segments. The abdominal segments are smooth. A few random granules may be present on the anterior part of the telson.

Figs 1–11. *Eubelum rusingaense* sp. nov. Lower Hiwegi Series, Lower Miocene of Rusinga Island, Kenya; all ×5. 1, 2, anterior and left lateral views of **holotype,** In.61025. 3–11, paratypes. 3, ventral view of In.61026, to show triarticulate flagellum of left second antenna. 4, ventral view of In.61027, to show leg bases. 5, dorsolateral view of In.61028, to show ommatidia of right eye. 6, left lateral view of In.61029. 7, ventral view of In.61030, to show clypeus and schisma. 8, ventral view of In.61031, to show coxopodite ridge. 9, ventral view of In.61032, showing imperfect preservation of legs. 10, anterolateral view of In.61033, to show ommatidia of right eye. 11, anterolateral view of In.61034, to show partial enrollment.

Fig. 12. *Eubelum ignavum* Budde-Lund, 1899. Recent; 8000–9000 ft (2460–2775 m), Djem-Djem Forest, Ethiopia. Anterior view of BM(NH) Zool. Dept. no. 1949.2.2.235, ×5.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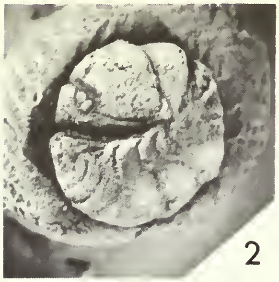
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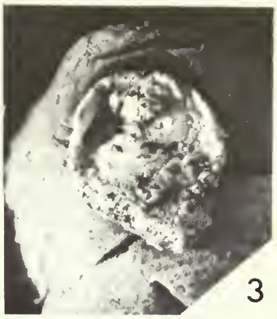
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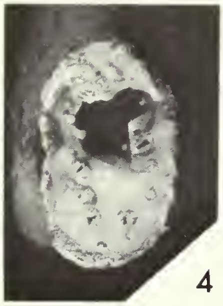
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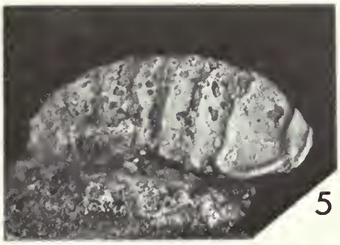
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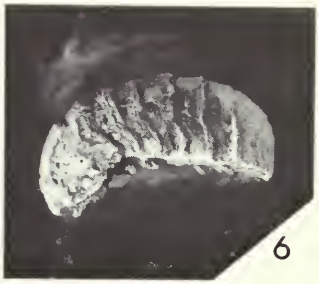
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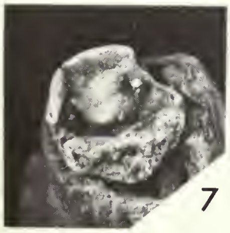
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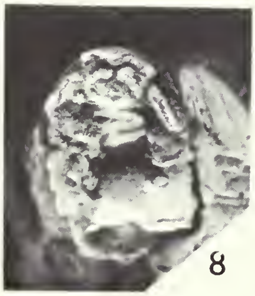
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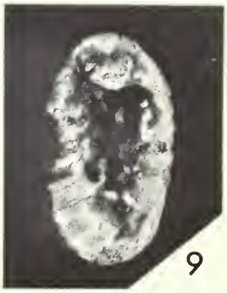
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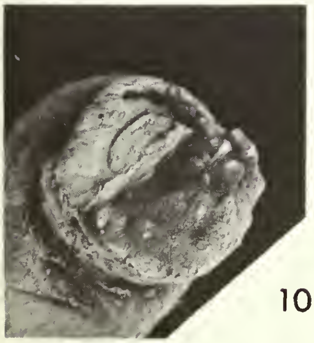
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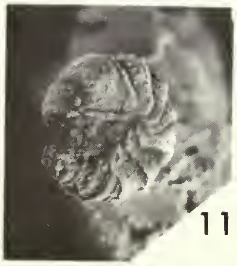
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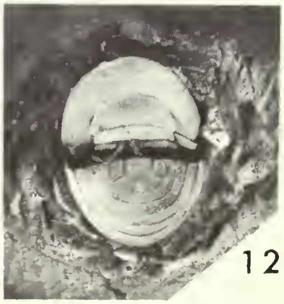
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DISCUSSION. The isopods are preserved in the round in a semi-transparent calcite. They occur with other, as yet undescribed, arthropods especially insects and myriapods. The nearest relations to the fossil species are *Eubelum ignavum* Budde-Lund, 1899 and *E. dollfusii* Budde-Lund, 1899. *E. rusingaense* differs from *E. dollfusii* by its continuous frontal line across the cephalon. *E. ignavum*, which has a continuous frontal line, differs because the posterior part of its profrons is not pushed up onto the vertex and its eye has only 14–15 ommatidia. The distal portion of the telson of both the Recent species has parallel sides and is relatively wider than the fossil species. *E. rusingaense* does have some similarities with the type species *E. lubricum* Budde-Lund from Zaïre, Congo Republic and Cabinda (Angola) (Ferrara & Schmalfuss 1976) but the telson is not so convergent, the larger eyes have 23–24 ommatidia, the escutcheon is much less prominent but broader, and it differs in the shape of the supra-antennal line. Van Name (1920 : 85) compared *E. asperius* with *E. ignavum*, but Arcangeli (1950) made *E. asperius* the type species of a new subgenus *Pseudethelum*, based on the two-jointed flagellum of the second antenna. Ferrara & Schmalfuss (1976) went further and suggested that after a thorough revision of the genus the *asperius* group would warrant generic separation from *Eubelum* s.s.

Enrollment. The specimens from Rusinga are found in many degrees of enrollment, from a flat to a relaxed arched condition; six specimens show a nearly complete enrollment with only a slight gape between the frontal line and the pleotelson. The coxopodite ridge of the first pereionite is ventrally grooved but, although complete closure would seem possible, none of the specimens show contact between the groove and the squared-off margins of the epimera of the fifth to seventh pereionites and first to fifth pleonites. The face is flattened and the escutcheon is well developed. The method and order of enrollment appears to be as in Vandel (1943 : fig. 10). When straight, the specimens can protrude the cephalon by a hinged movement along the posterior margin of the cephalon.

REMARKS. Although terrestrial isopods are not dependent on an aquatic environment, they are poorly adapted to resist desiccation and super-saturation. Their habits are governed by the need to avoid excesses, although they will move along a hydrocline towards the saturation point. Since their transpiration rate is greater than their normal uptake of water, the difference between the two rates has to be made up from moist substances taken up by mouth or by water taken directly through the body wall (Edney 1954). Their moisture requirements can be satisfied by a number of habitats, consequently isopods are not indicative of any particular one. *E. rusingaense* probably lived in a damp montane forest litter, but could have lived in moist open grassland, under stones or near a water margin. The genus *Eubelum* in East Africa is, today, confined to montane forest at fairly high altitudes, certainly above 2000 m, where there is a relatively high annual precipitation rate. The nearest modern relatives of *E. rusingaense*, *E. ignavum* and *E. dollfusii*, have so far only been found in the Ethiopian highlands between 7000 ft (c. 2150 m) and 9000 ft (c. 2775 m) in montane forest litter near water margins (Barnard 1940 : 365). Rusinga Island lay, before the Miocene, within the Kavirondo rift valley system at about 4000–4500 ft (1300–1350 m) (Shackleton 1951, Pulfrey 1960, Bishop & Trendall 1967). Andrews & Van Couvering (1975) deduced that the pre-uplift elevation of the sub-Miocene remnant surface was at about 1500 m. They further note that this is the lower limit of the montane forest. Their analysis of the fauna showed no clear predominance of any vegetational type, but indicated that large tracts of forest occurred in the immediate vicinity. If the distribution of the East African isopods was climatically controlled in the Miocene as it is now then the surface would have been at a somewhat higher altitude than has been previously suggested, i.e. within the montane forest belt at about 2500 m. *Eubelum* is not confined to the highlands of East and central Africa but occurs in the lowlands of West Africa. However, these largely belong to the *asperius* group, that is now thought to be generically separable from *Eubelum* s.s. Furthermore, Vandel (1945 : 226) considered that lowland species represented recent immigrants, whilst highland species were those that remained near the autochthon. This suggestion is supported by the close relationship between the new species and the Recent indigenous species.

Acknowledgements

I would like to thank Dr F. Ferrara, Florence, for help with the systematic position of the fossil within the Eubelidae.

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A re-evaluation of the fossil human calvaria from Singa, Sudan

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Synopsis

The first studies of the Singa calvaria concluded that it was an Upper Pleistocene 'proto-Bushman' fossil. More recently it has been suggested that it is a 'neanderthaloid' specimen or an anatomically modern specimen. This study concludes that the Singa calvaria is an unusual archaic *Homo sapiens* fossil, perhaps most closely related to the crania from Djebel Irhoud.

Introduction

The Singa calvaria (Fig. 1) was discovered by W. G. R. Bond in 1924, eroding from a caliche deposit within the 'Gezira clay' exposed in the west bank of the Blue Nile (Oakley, Campbell & Molleson 1977). The discovery was made in the Singa district of eastern Sudan, about 320 km south-east of Khartoum, and faunal and archaeological remains were also recovered, both at the Singa site and the related site of Abu Hugar, about 15 km further south (upstream). The collection of faunal material contained some extinct species including an antilopine, a porcupine (*Hystrix astasobae* Bate 1951) and a bovine allocated by Bate to *Homoioceras singae* Bate 1949 (Bate 1951). The allocation of the bovine fossils from Singa and Abu Hugar to an extinct species of long-horned buffalo has recently been questioned, and it appears probable that the holotype skull from Singa belongs to a short-horned buffalo (Gentry & Gentry 1978). Nevertheless, Bate's conclusion that the fauna from Singa and Abu Hugar is of Upper Pleistocene age, and perhaps dates from an earlier phase of the Upper Pleistocene, still stands (Bate 1951).

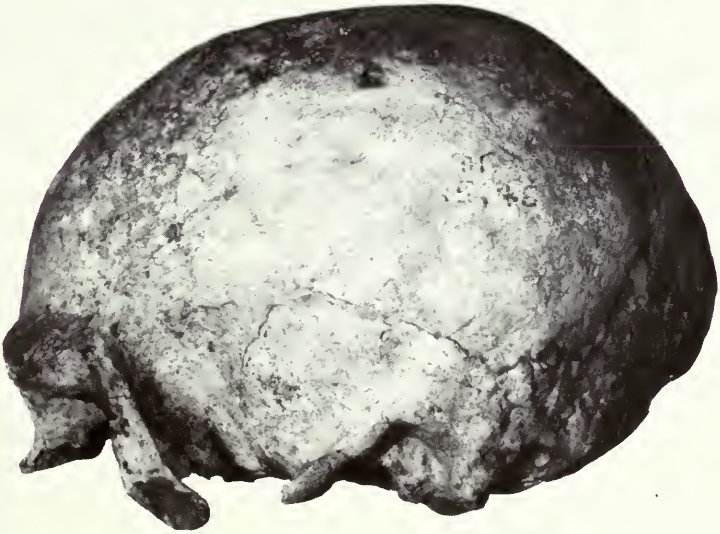

Fig. 1. Left lateral view of the Singa calvaria. BM(NH) Anthropology registration number M 15546. × ½.

Bull. Br. Mus. nat. Hist. (Geol.) **32** (1) : 77–83.

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Lacaille (1951) considered that the Singa and Abu Hugar implements had most affinity with the Middle Stone Age Proto-Stillbay industry of Lochard, Rhodesia, which would indicate on present dating evidence an earlier Upper Pleistocene age. However, Marks (1968) cautioned that the artefacts were nondescript, and although found in the same layer as the calvaria, were not necessarily of the same age. He agreed with Lacaille that some of the flakes might be 'Levallois' but remarked that Levallois flakes occurred in a variety of African Middle and Late Stone Age industries of widely-differing ages. He also commented that there were no grounds for comparison of the Singa artefacts with the Khormusan Levalloiso-Mousterian industry known from the Nile region. However, McBurney (1977) quoted a range of radiocarbon dates for the Khormusan from over 43 000 years BP (before present) to less than 20 000 years BP and suggested that the Singa calvaria might represent the population which produced what he considered to be 'the latest expression of the Mousterian so far known in the world'. Whiteman submitted a crocodile tooth from Abu Hugar for radiocarbon dating, which produced an age of 17 300±2 000 years BP. Whiteman and Oakley considered that this late Pleistocene radiocarbon age might be due to contamination from the limestone in the Abu Hugar deposit or from the river Nile which regularly flooded its banks in the area (Whiteman 1971). The relatively low radiocarbon age is also inconsistent with relative dating analyses which apparently confirmed the association of the Singa calvaria and the Abu Hugar fauna, but revealed that the bones contained only a negligible amount of collagen (Oakley *et al.* 1977).

Review of previous studies of the Singa calvaria

The first description of the Singa calvaria was published by Woodward (1938), who concluded that the specimen was a brachycephalic variant of the 'Boskop type' of *Homo sapiens* known from the later Pleistocene of southern Africa. Modern Khoisan (Bushman) populations were regarded by Woodward as 'degenerate' survivors of this Boskop race. Wells (1951) compared the Singa calvaria with a wider range of Upper Pleistocene hominids, but similarly concluded that the Singa fossil was a north African variant of the proto-Bushman stock already known from sites such as Boskop and Matjes River. Briggs (1955) accepted its pre-Bushman affinities but also suggested that the Singa calvaria was comparable to the 'type C' male crania from the late Pleistocene/Holocene site of Afalou in Algeria. Anderson (1968) discounted any relationship between the Singa fossil and populations such as those represented at Afalou, and he emphasized that the latter groups were instead clearly linked to European Upper Palaeolithic and Mesolithic populations. A similar view was taken by Greene & Armelagos (1972), who compared the Singa calvaria with the Wadi Halfa Mesolithic crania from northern Sudan. They also saw little resemblance between the Singa fossil and 'boskopoid' and 'bushmanoid' fossils from southern Africa. However, Wells (1972) reasserted that such a relationship existed, and suggested that the Singa fossil might be a paedomorphic descendant of the earlier Upper Pleistocene Omo (Kibish) population.

Tobias, however, noted that the supposed 'bushmanoid' characters of the Singa specimen were restricted to the rear of the vault, whereas the anterior part of the calvaria was more archaic, even resembling the Broken Hill cranium in certain details (Tobias 1968). In a more extensive study, Brothwell (1974) also questioned the Khoisan features of the Singa fossil and suggested that its unusual cranial shape might be the result of a longitudinal growth defect affecting the parietal bones, producing a cranial shape which superficially resembled that of Bushman skulls. The cranial contours of the Singa specimen were compared to those of other Pleistocene crania, and the comparisons suggested that the Singa calvaria most resembled archaic (i.e. not anatomically modern) *Homo sapiens* fossils such as the Gibraltar neanderthal cranium. Brothwell's data on cranial measurements were used in a multivariate principal component analysis conducted by Andrews, and the Singa specimen was placed as very distinct from various fossil and Recent Bushman crania as well as from a small sample of other Recent African crania (Brothwell 1974). Instead the analysis linked it with the Broken Hill cranium, but this was the only archaic *Homo sapiens* fossil included in the analysis from a range of relevant specimens. Brothwell concluded that the overall cranial morphology of the Singa calvaria lay closer to that of early Upper

Pleistocene crania from Europe, Asia and Africa than to late Pleistocene and Recent Khoisan specimens. He also suggested that the Singa fossil might represent a hybrid of 'neanderthaloid' and anatomically modern populations. However, Rightmire (1975) stated that in his view the Singa calvaria was not 'neanderthaloid' nor closely related to proto-Bushman or Bushman material from southern Africa. He agreed with Wells (1972) that it might be related to the Omo (Kibish) material, but concluded that it was probably a late Pleistocene example of robust but anatomically modern man.

A new study of the Singa calvaria

None of the studies of the Singa specimen have compared it in both metrical and morphological characteristics with a full range of relevant Upper Pleistocene crania as well as a range of more recent African material. In a multivariate study of Middle and Upper Pleistocene hominid crania using Mahalanobis' generalized distance statistic (D^2) (Rao 1952 : 246), the Singa calvaria was compared with a wide range of other fossil crania (Stringer 1974). It was concluded that the specimen was not closely related metrically to modern *Homo sapiens*, but instead was more similar to the *Homo erectus* fossils from Ngandong (Java) and to archaic *Homo sapiens* crania such as the Broken Hill fossil and the European and south-west Asian Neanderthals. However, at that time it was not possible to use, in comparison, data from certain relevant fossil crania nor from large samples of Recent African populations (including Bushmen). Additionally, the multivariate analyses used by Brothwell (1974) and myself (Stringer 1974) had not distinguished factors of size from those of shape in assessing multivariate distances. The size and shape statistic of Penrose (1954) does allow such distinctions to be made whilst accurately reflecting true differences in size and shape (Corruccini 1973). This method of analysis is utilized here, modified by the use of logarithms of the raw cranial data rather than standardized data. This approach can be shown on theoretical and empirical grounds to give a shape distance which more truly reflects proportional change in shape, and it also avoids the problem of standardizing data from small or metrically divergent samples.

The computation of the Penrose size and shape statistic in the case for P variables is based on the equation

$$\underbrace{\frac{1}{\mathrm{P}} \sum d_i^2}_{\text{total distance}} = \underbrace{\bar{d}^2}_{\text{size}} + \underbrace{\frac{1}{\mathrm{P}} \sum (d_i - \bar{d})^2}_{\text{shape}}$$

where $d_i = X_i - X_i'$, X_i refers to log i^{th} measure on the Singa calvaria and X_i' to log i^{th} measure on another specimen or group. The total distance and size distance are calculated, and the shape distance is obtained by subtraction. Size distances which were negative before squaring are plotted separately in the results from those which were positive.

Eleven cranial measurements (glabello-occipital length, maximum cranial breadth across parietals, bistephanic, biauricular and biasterionic breadths, frontal chord and subtense, parietal chord and subtense, and occipital chord and subtense) were taken on a range of Middle and Upper Pleistocene crania (samples generally as Stringer 1974). It was also possible to include for the first time comparative cranial data from the south-west Asian Upper Pleistocene sites of Qafzeh (where I have combined data from crania 6 and 9 with data from the comparable Skhul 5 specimen) and Shanidar (where I have combined data from Shanidar 1 with data from the comparable Amud 1 fossil to form an Asian Neanderthal group). Data from the robust Achegour 1 Mesolithic cranium were also included as this was representative of a late Pleistocene/early Holocene mid-Saharan population (Oakley *et al.* 1977). Large comparative samples of Recent African male and female crania were also included (sample size for each sex numbered between 34 and 58 individuals) using data collected by Howells (1973). However, it was not possible to use comparative data from the Sudanese Wadi Halfa Mesolithic crania (Greene & Armelagos 1972) since a different series of measurements were taken.

The results of the size and shape analysis with the Singa calvaria as reference specimen are displayed in Fig. 2. It can be seen that the specimens and populations generally regarded as 'anatomically modern' are all very distinct in shape from the Singa fossil, although Bushman crania are closest to it of the Recent groups. Omo (Kibish) 1 and the Asian Neanderthal sample are also quite distant from the Singa specimen. However, the *Homo erectus* samples from Peking (Choukoutien) and Ngandong (Java), the archaic *Homo sapiens* crania from Djebel Irhoud, Saccopastore, Broken Hill and Omo (Kibish) 2, and the European Neanderthals, are all relatively close to the Singa calvaria in shape. Thus the Singa specimen apparently displays metrical features of *Homo erectus* and archaic *Homo sapiens.*

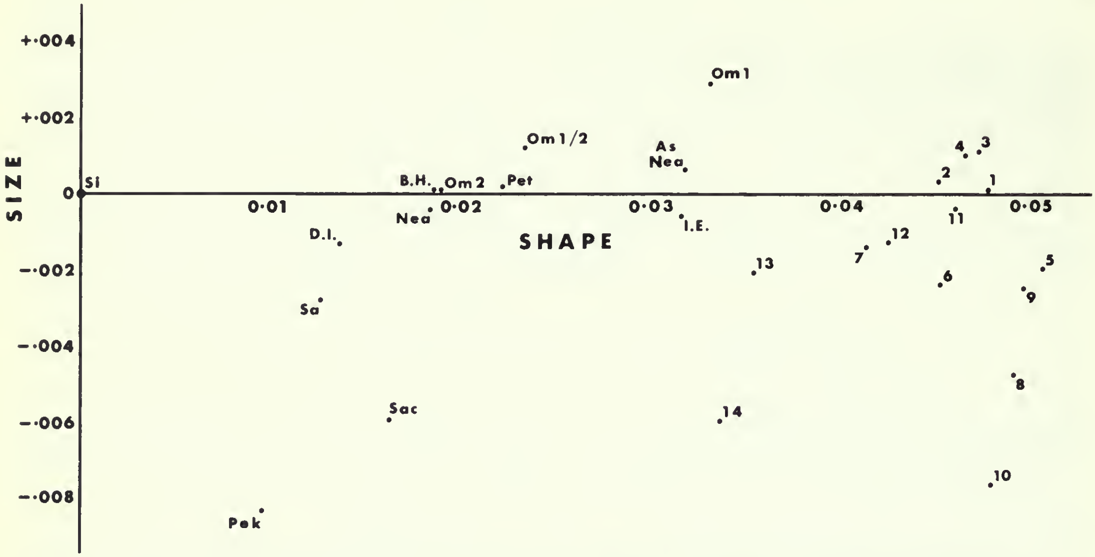

Fig. 2. Result of Penrose size and shape analysis using Singa calvaria as reference specimen. 1 – Qafzeh 6, 9 and Skhul 5; 2 – European Upper Palaeolithic group; 3 – North African Mesolithic group; 4 – Achegŏur (Niger); 5, 6, male and female Egyptian; 7, 8, male and female Teita (Kenya); 9, 10, male and female Dogon (Mali); 11, 12, male and female Zulu; 13, 14, male and female Bushman. Si – Singa; D.I. – Djebel Irhoud 1; So – 4 Ngandong (Solo) crania; Pek – 4 Peking (Choukoutien) crania; Sac – Saccopastore 1; Nea – European Neanderthal group; B.H. – Broken Hill; Om – Omo (Kibish) crania, treated separately and as a group; Pet – Petralona; As Nea – Amud 1 and Shanidar 1; I.E. – Iwo Eleru (Nigeria).

Any attempt to classify the Singa fossil must take into account morphological, as well as metrical, characteristics. The shape analysis (Fig. 2) could not accurately reflect overall cranial morphology since the data employed are predominantly measured lengths of chords and subtenses in the sagittal plane and breadths of the lower part of the cranial vault. Shape resemblance between the Singa and *Homo erectus* specimens is a reflection of a short, relatively low cranial vault, broad at the base, a very short, flat parietal arch, and a protruding occipital bone. Differences in shape are primarily caused by the larger occipital chord, parietal breadth and frontal dimensions of the Singa fossil. The much greater size of the Singa fossil is particularly marked in comparison with the Peking *Homo erectus* crania (Fig. 2). This is obviously related to the greater cranial volume of the Singa specimen. Previous estimates of the cranial capacity of the Singa fossil calculated from external measurements ranged from 1550 to 1600 ml (Wells 1951) and my own calculations confirm these figures. Using millet seed to measure the endocranial volume not occupied by matrix gave a value of approximately 1100 ml, and examination of radiographs suggests that there is at least 300 ml of matrix remaining within the calvaria. It is hoped that the endocranial surface can eventually be cleaned to obtain a better estimate of endocranial volume, but it is clear that the cranial capacity of the Singa specimen lies well outside the range of 915–1255 ml measured for eleven of the Peking and Ngandong crania (Day 1977). The Singa calvaria also differs from *Homo erectus* crania in a whole range of morphological features. The supraorbital torus in the Singa fossil is strongly developed laterally but does not form a thick continuous structure. The occipital bone, although projecting, is not strongly angulated, and the occipital plane is long compared to the nuchal plane, which is poorly defined. The occipital torus conforms to the *Homo sapiens* pattern, and those measurements of occipital and parietal thickness which can be taken fall within the range of values for *Homo sapiens* rather than for *Homo erectus*. Additionally the cranial vault displays none of the angularity and sagittal keeling characteristic of *Homo erectus* and Middle Pleistocene archaic *Homo sapiens* crania.

In a recent study of Pleistocene hominids I investigated the use of angles and indices as a means of discriminating between *Homo erectus*, archaic *Homo sapiens* and anatomically modern *Homo sapiens* crania (Stringer 1978). Although there was often an overlap in ranges of values between the groups, it was usually possible to assign isolated specimens to one or other of these groups on the basis of their cranial angles and indices. Table 1 shows which angles and indices could be determined for the Singa calvaria, and the group ranges within which the values for the Singa specimen fall (indicated by +). The nasio-frontal angle which measures the medial projection of the upper face shows no discrimination in this case, but the other values appear to indicate a resemblance to archaic *Homo sapiens* crania. The only exception, the low value for the bregma angle, is related to the relatively short basion–nasion length of the Singa calvaria. However, a relatively short basion–nasion length is also found in the Broken Hill cranium which has the lowest value for the bregma angle found in archaic *Homo sapiens* crania, and which also falls within the modern range of values for this angle. It seems certain that the Djebel Irhoud 1 fossil (which lacks the basion) would also have had a similarly low value for the bregma angle, suggesting that the Singa calvaria is in fact close to African archaic *Homo sapiens* crania in this feature.

Table 1. Classification of the Singa calvaria using ranges of variation in angles and indices for Pleistocene fossil hominid crania (position of Singa indicated by +)

	Nasiofrontal angle	Bregma angle	Nasion–bregma angle	Frontal angle	Parietal angle	Occipital angle	Bregma–asterion chord / Biasterionic breadth
Homo erectus (Peking and Ngandong)	+				+	+	+
Archaic *Homo sapiens* (includes Petralona, Broken Hill and Neanderthals)	+		+	+	+	+	+
Anatomically modern *Homo sapiens* (includes Qafzeh and Skhul)	+	+		+			

There are other characteristics in which the Singa calvaria resembles archaic rather than anatomically modern *Homo sapiens*. The temporal bone is relatively low and robust, the supraorbital torus is broad and well-developed laterally and the interorbital area and malars are strongly built (Tobias 1968, Brothwell 1974 and my own observations). The mastoid processes are small and there is a well-developed occipitomastoid crest, as in many archaic *Homo sapiens* crania (Stewart 1964). But on the other hand the height of the occipital plane compared to the length of the nuchal plane is relatively large, as in anatomically modern *Homo sapiens*.

Combining the metrical and morphological data given here it seems likely that Tobias (1968) and Brothwell (1974) are correct in questioning the proto-Bushman and modern affinities attributed to the Singa fossil. It is probably a relatively late archaic *Homo sapiens* specimen with an unusually short parietal arch which has affected the overall cranial shape (Brothwell 1974). Its affinities are more likely to lie with late archaic *Homo sapiens* fossils such as those from Omo (Kibish) and Djebel Irhoud rather than with earlier specimens such as the Broken Hill cranium. Whilst there seem to be no Upper Pleistocene crania which match the Singa calvaria closely in metrical characteristics it may be significant that the Djebel Irhoud 1 specimen is closest in overall Penrose (1954) distance (size+shape) to the Singa fossil. Both Djebel Irhoud 1 and the second specimen from the site are short broad crania with high frontal bones and relatively small brows compared with many other archaic *Homo sapiens* crania (Ennouchi 1968). Like the Singa fossil they also have relatively short deep infratemporal fossae, small mastoid processes and a large cranial capacity. It seems possible that the Singa calvaria in fact represents an unusual individual specimen drawn from a comparable archaic *Homo sapiens* population which lived in Sudan during the Upper Pleistocene.

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New species of Protorthoptera and Protodonata (Insecta) from the Upper Carboniferous of Britain, with a comment on the origin of wings

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Synopsis

Narkeminopsis eddi gen. et sp. nov. (Protorthoptera) and *Erasipteron bolsoveri* sp. nov. (Protodonata) are described. The use of wings for functions other than flight in the earliest insects is discussed.

Origin of wings

New insect specimens from the Carboniferous of Britain are not common. The species of Protodonata from Derbyshire described here is one of the oldest Carboniferous fossil insects found in Britain, the only earlier British fossil insect being the wingless *Rhyniella* from the Devonian. The two new species described show the complex wing venation typical of these early winged insects. With such specialized forms flying, we have to look further back in time for the origins of wings. Even if *Rhyniella* is a genuine fossil insect, and this is still disputed (Crowson 1970), it is unlikely to have been ancestral to the flying forms since the proponents of its insect affinities suggest that it is a collembolan.

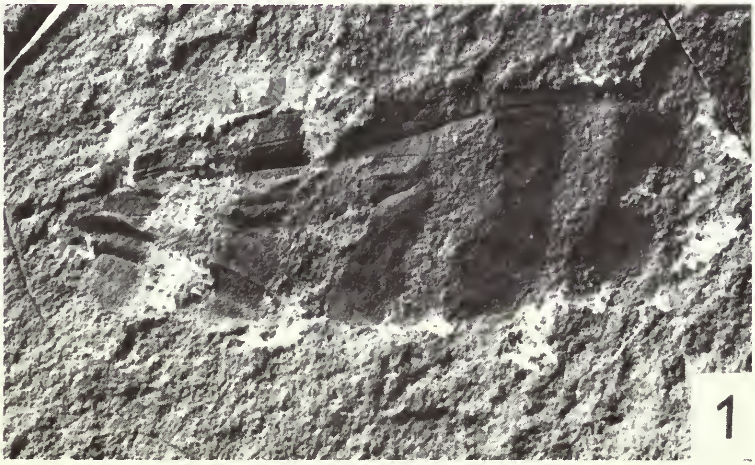

Fig. 1. *Narkeminopsis eddi* gen. et sp. nov. Upper Carboniferous (Westphalian D), Radstock, near Bristol. Wing, 25·5 mm × 9 mm.

There are no insect fossils yet known for the critical period in insect evolution from the Upper Carboniferous back into the Devonian, when the wingless *Rhyniella* occurs; thus we can still only speculate on the factors which stimulated the production of wings. However, I believe there is evidence available from Recent insects which has been overlooked and which can be used to support a multiple-factor theory for the origin of wings.

With the discovery of the circulation of the haemolymph in the wing veins of insects, first reported in 1934 by Yeager & Hendrickson, we can consider that wings may have evolved not

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only for flight, and perhaps gaseous exchange as suggested by Portier (1930), but also as heat-exchangers. Clench (1966) describes the use of wings in butterflies for heat exchange, and Gillett (1971) also suggests an alternative to their use in flight.

If these facts are applied to the earliest insect, it is possible to consider that outgrowths of the body wall, which would have been developed to help increase the surface-area/volume ratio, could have been used as a sort of aerial gill and heat-exchanger. They would need some musculature to move them for orientation, or even to allow more efficient heat or gaseous exchange. The outgrowths or 'proto wings' could then have been developed concurrently with flight, which became their most important function. It is not suggested that this is directly in line with the tracheal-gill theory (see Wigglesworth 1976) for which an aquatic stage is postulated, but merely that flight does not have to be considered as the only function of the early 'wing'.

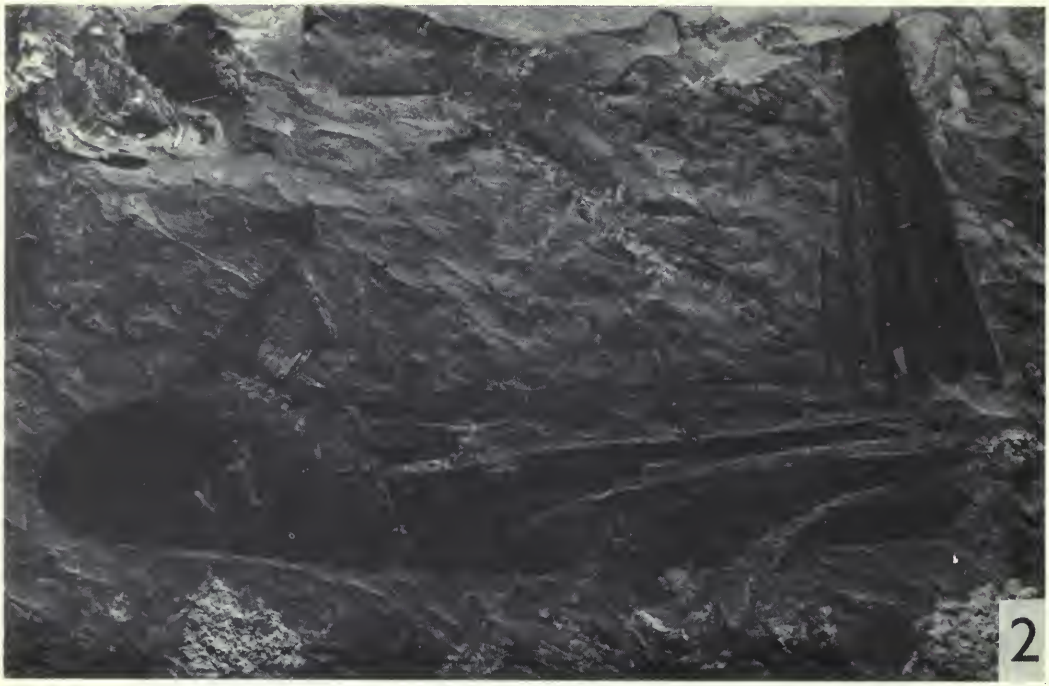

Fig. 2. *Erasipteron bolsoveri* sp. nov. Upper Carboniferous (Westphalian A), Derbyshire. Wing, 87 mm × 12 mm.

Systematic descriptions

Order **PROTORTHOPTERA**

(including Protoblattoidea and Paraplecoptera)

Carpenter (1966) considered there were few essential differences between species formerly placed in the Protoblattoidea and Paraplecoptera, and those in the Protorthoptera; the latter name has priority. The species described below is placed in the Protorthoptera following Carpenter (1966), although the limits of the order still need to be defined.

Family **NARKEMIDAE** Handlirsch, 1911

Professor Carpenter (in litt.) suggests that *Narkeminopsis* gen. nov. and *Narkemina* Martynov are sufficiently distinct from the poorly-preserved *Narkema taeniatum* Handlirsch, the type of the family Narkemidae, to be placed in a new family. *N. taeniatum* does show bandings of light and dark across the wing as in *N. eddi* sp. nov., but the dark bands are much narrower and there are differences in the origin of the median veins. From *Narkemina angustatum* Martynov (the type-species of *Narkemina*) *N. eddi* differs in the narrower costal area and fewer cross-veins, and has a longer basal part to the median vein (Carpenter, in litt.). The basal part of the wing of *N. eddi* (Fig. 3) clearly shows the origin of CuA and CuP. Pending further research, no new family is proposed for the new genus *Narkeminopsis*, which is provisionally placed in the Narkemidae (Upper Carboniferous).

Genus ***NARKEMINOPSIS*** nov.

Type-species. *Narkeminopsis eddi* sp. nov.

Diagnosis. Forewing. Costal margin smooth, gently curved. Sc with several unbranched oblique veins. Sc terminates on R_1. Rs forks from R roughly halfway to termen. Costal margin narrower, cross-veins less numerous and basal part of median vein shorter than in *Narkemina* Martynov.

Hindwing unknown.

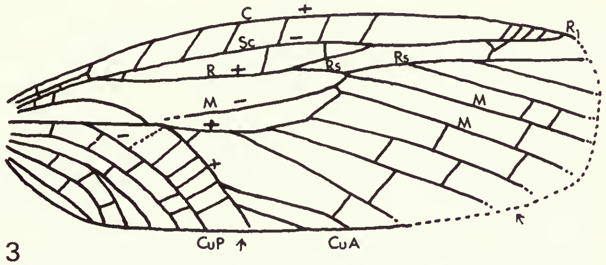

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Fig. 3. *Narkeminopsis eddi*, wing venation, diagram. +convex veins; — concave veins.

Narkeminopsis eddi sp. nov.
(Figs 1, 3)

Diagnosis. Forewing. 25·5 mm × 9 mm. Wing impression (no counterpart) preserved upside down. Rs with several branches. Main wing cells distinctly spindle-shaped. MA and MP present, apical parts missing. CuA with several branches, CuP single to wing margin. Cross-veins prominent. Archedictyon present. Wing markings prominent as strong, dark, parallel cross-bands, each approximately 2 mm wide, at a slight angle across wing.

Holotype. BM(NH) In.64531. Upper Carboniferous (Westphalien D); Radstock, nr Bristol, Avon; collected by E. Jarzembowski.

Discussion. The archedictyon on the wing is only faintly visible and can be seen between the branches of CuA and along part of the costal margin. The bands of darker colour are well defined and relatively smooth while the lighter areas are rougher, suggesting a more delicate (? less sclerotized) membrane which has virtually disappeared, leaving just the impressions of the wing veins. The transverse banding may well represent part of the original wing pattern.

Order **PROTODONATA** (Meganisoptera)

Diagnosis. Dragonfly-like insects which lack the nodus, arculus and pterostigma of typical Odonata.

Family **ERASIPTERIDAE** Carpenter, 1939

Diagnosis (modified after Carpenter, 1939). CuA present, reduced. Anal-crossing vein between CuP and 1A. MP absent. Archedictyon present. Basal part of costa of forewing toothed. One included genus.

Genus *ERASIPTERON* Pruvost, 1933

Type-species. *Erasipteron larischi* Pruvost 1933, by monotypy. Upper Carboniferous (Namurian C), Czechoslovakia.

Diagnosis. Relatively few cross-veins. Sc roughly half length of forewing. Rs strongly branched in apical area of wing.

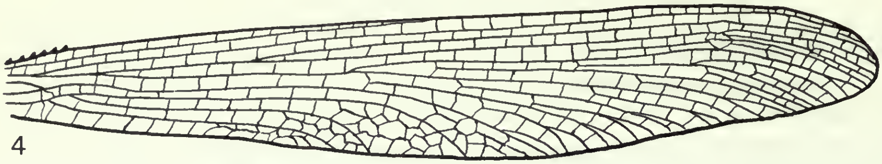

Fig. 4. *Erasipteron bolsoveri*, reconstruction

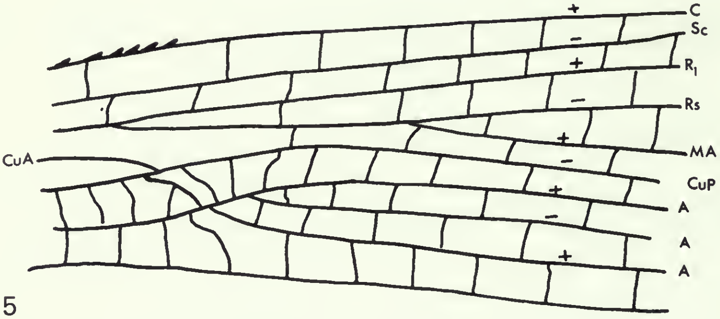

Fig. 5. *E. bolsoveri*, basal third of wing, venation diagram. +convex veins; — concave veins.

Erasipteron bolsoveri† sp. nov.
(Figs 2, 4, 5)

Diagnosis. Forewing. 87 mm × 12 mm. No pattern visible. Concave and convex veins clear (Fig. 5). R_1 terminates near wing apex. Rs sharply curved down at apex. Rs and MA fork one-third from base. Anal veins curved in basal area. Anal cells simple, single row.

Hindwing unknown (but see Discussion).

Holotype. BM(NH) In.64532. Upper Carboniferous (Westphalien A); Derbyshire, Bolsover deep hard seam, at 586 m, approx. 15 cm above seam. Collected by M. Spencer.

Discussion. This species can be separated from *E. larischi* by the presence of cells in the area formed by the anal-crossing vein, and by the simple arrangement of cells in the basal part of the anal area. An incipient nodus is supposed to be present in *E. larischi* (Carpenter 1939; Kukalová 1964); no trace of a nodus can be seen in *E. bolsoveri*, but there is some damage to this part and the presence of a nodus cannot be entirely ruled out.

The specimen from Derbyshire is the second species of the genus *Erasipteron* Pruvost, family Erasipteridae *sensu* Carpenter (1939). The type-species, *Erasipteron larischi* Pruvost, was described from a single hindwing from the Upper Carboniferous (Namurian C) of Czechoslovakia, and redescribed by Kukalová (1964); the new species is based on a forewing.

The type specimen of the new species probably consists of two wings, although only one is immediately visible. The two wings lie exactly one above the other, separated by a matrix of 0·5–1·0 mm. These wings were broken in the basal third, the two parts lying at right-angles to one another (Fig. 2). The double nature of the fossil can be seen one-third from the apex, where some of the overlying wing has been removed. The lower wing matches exactly the size and vein positions of the upper wing. There is a trace of the underlying wing near the base, but this is not as clear as the apex.

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† This name has already appeared a number of times in the popular press, but without formal diagnosis.

Two possibilities have to be considered. A single wing may have become separated into an upper and lower wing membrane and the space between filled up like a sac; the resulting 'double wing' would therefore be only the upper and lower membranes of one wing. Alternatively there are two wings which have been fossilized exactly together.

From an examination of the specimen the latter explanation seems more probable; for example, the thickness of the matrix between suggests two wings rather than an upper and lower surface of one wing.

It is difficult to tell from the amount of the lower wing revealed whether it is a fore or hind wing, but it is, in the apical part at least, an exact replica of the upper wing but with most of the convex–concave vein system flattened out. It is possible that the convex–concave system is identical with the upper wing. If this is correct then the lower wing is likely to be the hindwing from the same side as the upper wing (which I regard as a forewing), thus indicating that the insect was homoneurous, with a simpler anal area than in *E. larischi*. This would provide conclusive evidence of the two species being generically distinct. Unfortunately this hypothesis is based on the condition of the convex–concave state of the lower wing, which is not clearly visible.

With the information available I do not propose to describe a new genus but to redefine *Erasipteron* Pruvost. It is possible that there were differences between the forewings and hindwings in species of *Erasipteron*, which would explain some of the discrepancies between *E. larischi* (hindwing) and *E. bolsoveri* (forewing), but data are not available to support or contradict this. The new species may well be homoneurous but the facts are inconclusive.

E. bolsoveri is the most complete specimen of the larger, dragonfly-like Protodonata found in Britain, with an estimated wingspan of nearly 200 mm (8 inches), larger than any extant species.

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Synopsis

The Carboniferous (Dinantian and low Namurian) rocks of west Fermanagh, south of Lower Lough Erne, are correlated with strata from surrounding areas in north-western Ireland and divided into formations dated faunally and by the recognition of major sedimentary cycles. The proposed Ballyshannon Group consists of marine shales and limestones with two deltaic sandstone intercalations; the Dartry Group (new name) is entirely marine and includes a mud-mound 'reef' phase; the Leitrim Group is of mixed marine, intertidal, lagoonal and deltaic sediments and includes sabkha deposits which may be correlated with those of eastern Canada.

Introduction

Since 1952 the Carboniferous geology of several areas of north-west Ireland has been described, but west Fermanagh has remained largely neglected since the original map (sheet 44, 1884) of the Geological Survey of Ireland and the Memoir (Symes & Wilkinson 1886) were published. The region investigated lies between Lower Lough Erne and the borders of counties Leitrim and Cavan (Fig. 1). Our purpose is to describe those features of the Carboniferous succession in the area which allow these rocks to be interpreted in terms of palaeoenvironments and permit their correlation with adjacent areas and with the Major Cycles of sedimentation described by Ramsbottom (1973).

This paper results from work carried out by the authors indpendently from 1962 to 1974.

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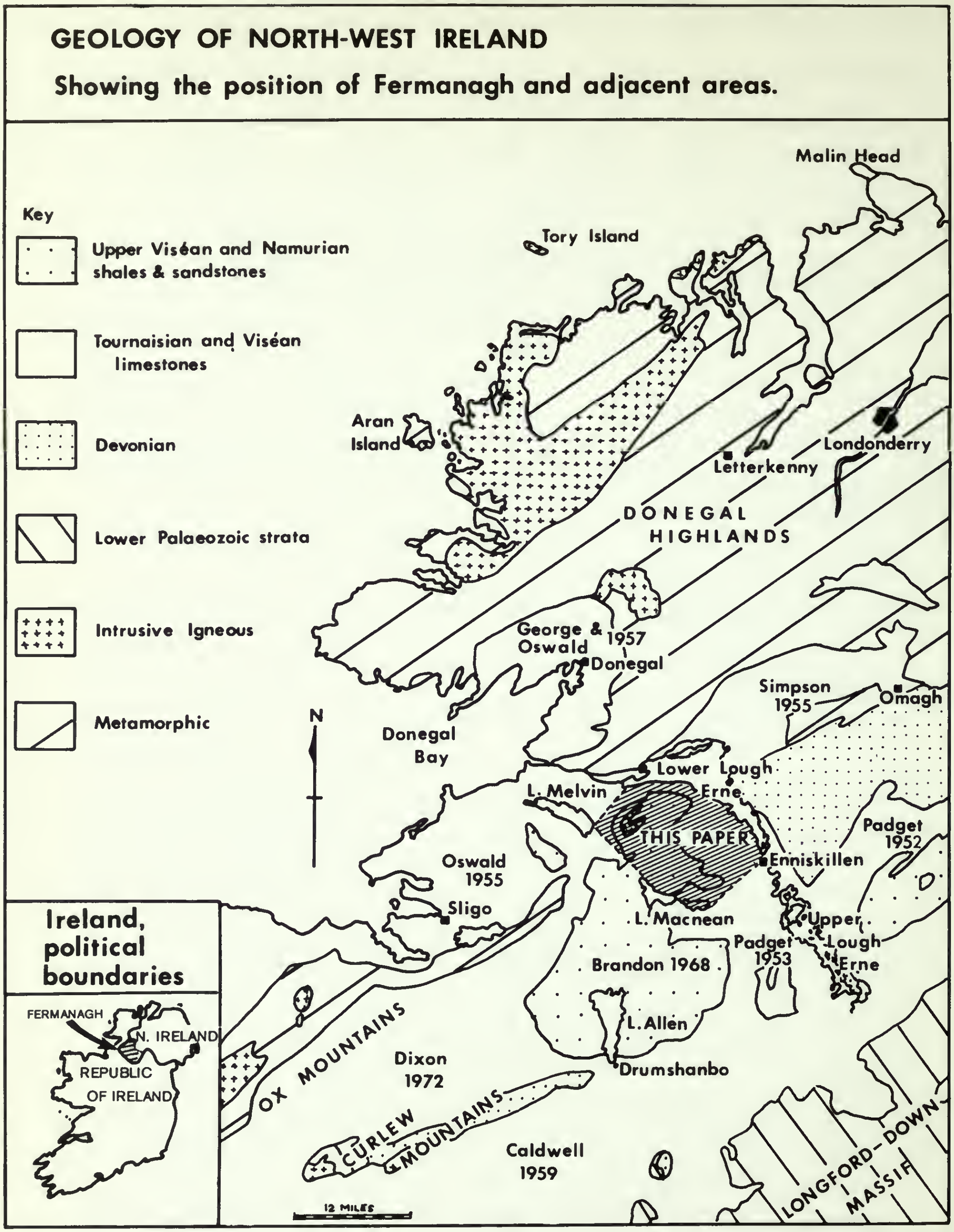

GEOLOGY OF NORTH-WEST IRELAND
Showing the position of Fermanagh and adjacent areas.
Key
Upper Viséan and Namurian shales & sandstones
Tournaisian and Viséan limestones
Devonian
Lower Palaeozoic strata
Intrusive Igneous
Metamorphic
N
Malin Head
Tory Island
Aran Island
Letterkenny
Londonderry
DONEGAL HIGHLANDS
George & Oswald 1957
Donegal
Donegal Bay
Simpson 1955
Omagh
Lower Lough Erne
L. Melvin
THIS PAPER
Enniskillen
Padget 1952
Oswald 1955
Sligo
L. Macnean
Upper Lough Erne
Padget 1953
Brandon 1968
L. Allen
Drumshanbo
OX MOUNTAINS
Dixon 1972
CURLEW MOUNTAINS
Caldwell 1959
LONGFORD-DOWN MASSIF
12 MILES
Ireland, political boundaries
FERMANAGH
N. IRELAND
REPUBLIC OF IRELAND

Fig. 1. Generalized geological map of north-western Ireland showing the area described herein together with the names of authors (with dates) who have described the surrounding regions. See also Figs 5 and 6. (After Geological Survey of Ireland, 1962.)

T. R. M. is generally responsible for the Leitrim Group and C. H. C. B. for the older strata. During this time we have described elements of the faunas: brachiopods by Brunton (1965, 1966*a*, *b*, 1968), fish by Gardiner & Mason (1974), while bryozoans have been studied by Tavener-Smith (1965, 1973). A small syncline, preserving the youngest strata, has been described by Brandon (1972), and Wilson (1964) discussed some of the large Tertiary dykes in the area. Sheridan (1972) has presented a review of work on the Upper Old Red Sandstone and Lower Carboniferous rocks of north-west Ireland, in which he provided some useful information on a borehole sunk in west Fermanagh which penetrated to unexposed marine Tournaisian rocks.

Lower to middle Viséan strata mainly occupy areas of low ground below about 150 m and are not well exposed. The uplands to the south provide extensive dip and scarp exposures in the mid- to upper Viséan limestones and sandstones, although the interbedded and overlying shales, which extend into the Namurian, are commonly limited to stream-section exposures.

The exposures in west Fermanagh display the succession more completely than those of adjacent areas and four major cycles of transgression and regression from low Viséan (V1b) up to the low Namurian (E1) are recognized. Most of the formation names are derived from the areas of Sligo, described by Oswald (1955), or Leitrim studied by Brandon (1972), but we introduce new stratigraphical Group names.

After completion of this work the Geological Society of London published its report on 'A correlation of Dinantian rocks in the British Isles' (George *et al.* 1976). This proposed regional stage names corresponding to the six Major Cycles of Ramsbottom (1973), and we have added these names to Fig. 2. We have not emended our script since the stage names correspond to the cycles of sedimentation we discuss and because we disagree with the positioning of some of the cycle/stage boundaries suggested by George *et al.* for north-west Ireland. In general the cycles of sedimentation (Ramsbottom 1973) start with marine, commonly transgressive, sediments. The regional stages generally follow this concept, but in north-west Ireland George *et al.* (1976) place the start of some regional stages at the bases of sandstone sequences we believe to be of regressive, deltaic origin. Thus, there appears to be some inconsistency in the application of the stage boundaries and we feel it is inappropriate at present to define their positions stratigraphically in north-west Ireland; compare Fig. 2 with George *et al.* (1976: fig. 15).

Rock stratigraphical names

Groups

The generalized succession in west Fermanagh is illustrated in Fig. 2. The rock units from the Ballyshannon Limestone to the Dergvone Shale are here considered as formations. These are divided into three Groups: the Ballyshannon Group, from the base of Ballyshannon Limestone up to the top of the Mullaghmore Sandstone; the Dartry Group, which finishes at the base of the Meenymore Formation, and the Leitrim Group, a unit named by Brandon (1972) for the Meenymore to Dergvone Shale Formations but without a defined upper limit. (In his thesis of 1968 Brandon assigned strata from the Glenade Sandstone up to the younger Lackagh Sandstone to the Leitrim Group, and all units below this to what he called the Sligo Group, a name which hitherto remained unpublished.)

The Ballyshannon Group includes the oldest known Carboniferous rocks in north-west Ireland. These are commonly exposed as basal conglomerates of the Ballyshannon Limestone, at the base of the Bruckless Grits and Conglomerates in Co. Donegal, or as the Boyle Sandstone of the Carrick-on-Shannon area. The relatively abrupt change from the Mullaghmore Sandstone to the Benbulben Shale marks the base of the Dartry Group. Although there is no indication of unconformity between the two, the rocks of the Dartry Group are more consistently marine limestones than those of the Ballyshannon Group. Brandon (1972) mentions the Dartry Limestone Group, but without definition, and since we include formations other than the Dartry Limestone we omit Limestone from the Group name. Brandon's unpublished thesis name 'Sligo Group' could be used as a super-group to unite the Ballyshannon and Dartry Groups.

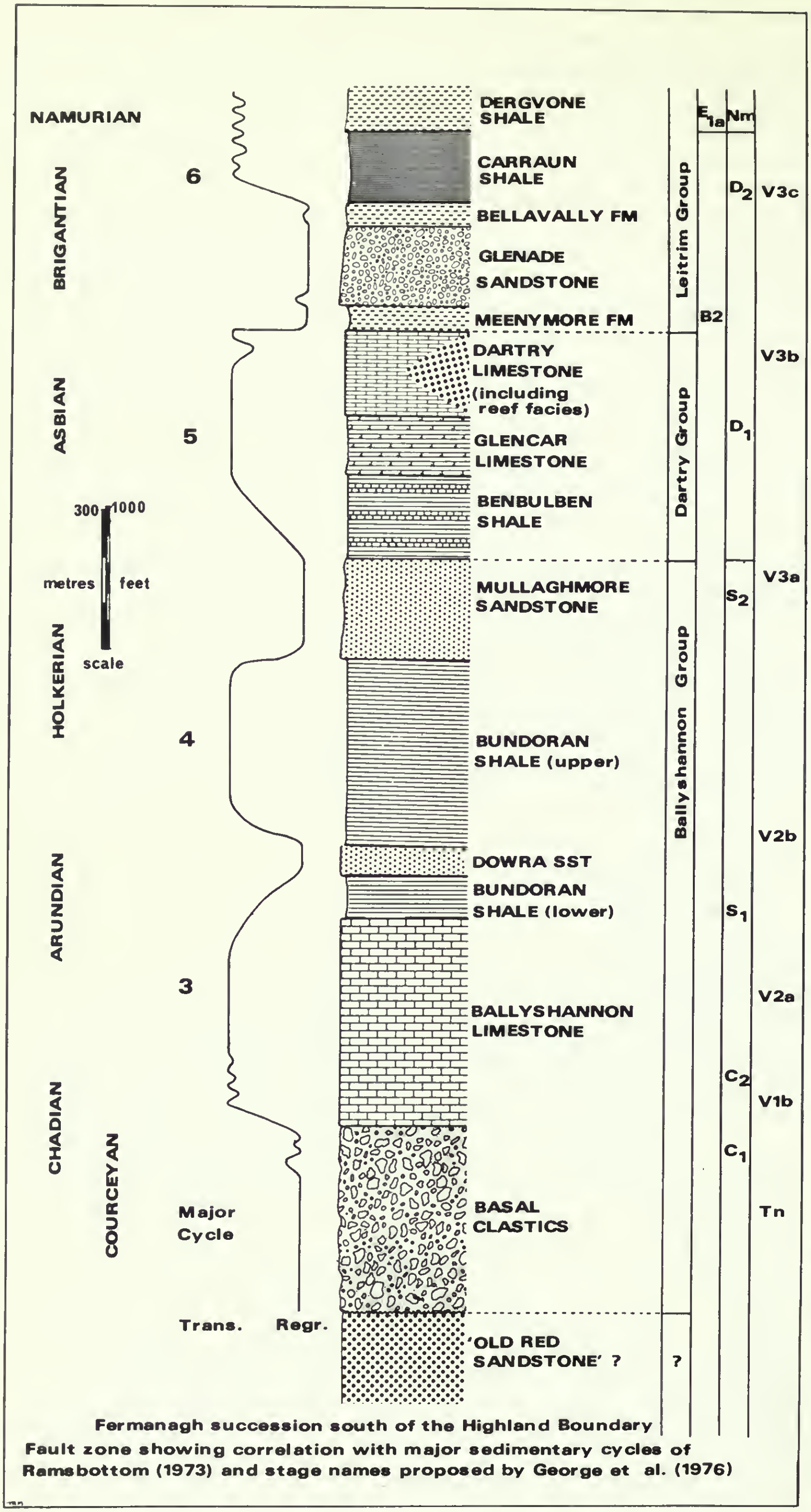

NAMURIAN
BRIGANTIAN
ASBIAN
HOLKERIAN
ARUNDIAN
CHADIAN
COURCEYAN
6
5
4
3
Major Cycle
Trans.
Regr.
300
1000
metres
feet
scale
DERGVONE SHALE
CARRAUN SHALE
BELLAVALLY FM
GLENADE SANDSTONE
MEENYMORE FM
DARTRY LIMESTONE (including reef facies)
GLENCAR LIMESTONE
BENBULBEN SHALE
MULLAGHMORE SANDSTONE
BUNDORAN SHALE (upper)
DOWRA SST
BUNDORAN SHALE (lower)
BALLYSHANNON LIMESTONE
BASAL CLASTICS
'OLD RED SANDSTONE' ?
Leitrim Group
Dartry Group
Ballyshannon Group
?
E1a
Nm
B2
D2
D1
S2
S1
C2
C1
V3c
V3b
V3a
V2b
V2a
V1b
Tn
Fermanagh succession south of the Highland Boundary Fault zone showing correlation with major sedimentary cycles of Ramsbottom (1973) and stage names proposed by George et al. (1976)

Fig. 2. The generalized geological succession in west Fermanagh south of the Highland Boundary Fault zone. The Basal Clastics and Dowra Sandstone are known in the area only from bore-hole evidence. In the north-west of the area the Ballyshannon Limestone rests directly on a Moinian basement, as shown in column F of Fig. 6, p. 104. Zonal correlations are indicated on the right.

The junction between the Dartry Limestone Formation and the Meenymore Formation varies from apparent conformity to erosional disconformity. This junction marks the base of the Leitrim Group but the youngest formations are not exposed in west Fermanagh.

Formations

The formation names follow the rock unit names proposed by Oswald (1955) up to the Dartry Limestone, and by Brandon (1972) from there upwards, with the following exceptions. Basal Clastics is used informally to denote the unexposed mixed basal Carboniferous rocks in west Fermanagh, known only from rather scant bore-hole information. Similarly, the Dowra Sandstone was named from Dowra no. 1 bore-hole, situated north-east of Lough Allen (Sheridan 1972). In this bore-hole the sandstone is 114 m thick from a depth of about 1270 m.

The type localities of the rock units described by Oswald (1955), and here accorded formation status, are as follows:

1. Ballyshannon Limestone – at Ballyshannon and the lower reaches of the river Erne, about 20 miles (32 km) north-west of Sligo.
2. Bundoran Shale – the foreshore and north side of Bundoran bay, about 16 miles (26 km) north-west of Sligo.
3. Mullaghmore Sandstone – the headland of Mullaghmore, 14 miles (about 23 km) north of Sligo.
4. Benbulben Shale – exposures on the lower slopes of the mountain bearing this name (spelt Benbulbin on many maps), about 6 miles (10 km) north of Sligo.
5. Glencar Limestone – the north side of Glencar where the formation is well exposed on steep southern flanks of the Benbulben range.
6. Dartry Limestone – this takes its name from the Dartry mountains, between the Benbulben range and Lough Melvin to the north. The formation occurs in most of the highland areas of counties Sligo and Leitrim and is well exposed to the south of Glanade Lough, between the Benbulben and Dartry ranges. The limestone is typically dark to light grey, often crinoidal, and chert-bearing in contrast to the lime mud mound facies (reefs of previous authors) developed within this formation.

The Meenymore Formation was described by Brandon (1972), who points out that it is equivalent to the oldest part of the Aghagrania Formation as described by West, Brandon & Smith (1968). In part, this formation is also equivalent to the Glenade Shales and Roscunnish Shales of Oswald (1955) and Caldwell (1959) respectively. The name is taken from Meenymore Townland, Glenboy, about 3 miles (5 km) ESE of Manor Hamilton, Co. Leitrim. The formation appears to be thin in this area and we suggest that the type locality, which has not yet been established, should be at the Aghagrania locality described by West, Brandon & Smith (1968) as the type locality of the Aghagrania Formation. The Aghagrania stream section lies about 1·5 miles (about 2·5 km) ENE of Drumshambo at the south end of Lough Allen, Co. Leitrim, where West, Brandon & Smith recorded 38·4 m of Meenymore laminated dolomite, limestones and shales.

The Glenade Sandstone was named by Oswald (1955) for the sandstones capping parts of the Dartry mountains north of Glenade. However, in this region no younger formations are known so its upper boundary cannot be established. Brandon (1972) used the term for equivalent sandstones in Co. Leitrim and estimated their thickness to be about 200 m in the Doagh Outlier region of west Fermanagh. We agree with this figure and believe our area provides a more complete sequence than exists in the Dartry hills. In Fermanagh the passage from the Meenymore to Glenade formations can be observed in sections of streams flowing north off the sandstone uplands, about 0·75 mile (1·2 km) south-west of Knockmore summit, 2·5 miles (4 km) WSW of Derrygonnelly village. The top of the Glenade Formation is difficult to demonstrate owing to poor exposures at the base of the Bellavally Formation. However, between the sandstone hill of Trustia (993 ft (303 m) high and 5 miles (8 km) slightly south of west of Derrygonnelly) and Doagh school (about 1 mile (1·7 km) to the north) there are stream exposures of Bellavally shales and Doobally sandstone. Our interpretation (Mason 1978) differs slightly from that of Brandon (1972), who did not recognize the shales and Doobally sandstones of the Bellavally Formation.

Stratigraphical succession

The Ballyshannon Group

Tournaisian. Rocks of proven Tournaisian age are not exposed in the area but are known from the deep bore-hole at Big Dog, about 9 km WSW of Derrygonnelly, from a depth of over 1500 m. This bore, drilled by Marathon Petroleum (Ireland) Ltd, penetrated between 500 and 600 m of sandstones, shales, thin limestones and anhydrites, thought on macro- and micropalaeontological evidence to be of Upper Tournaisian (Tn3c) age by Sheridan, Hubbard & Oldroyd (1967), before being abandoned while still in marine strata. This great thickness of mainly arenaceous Carboniferous sediment contrasts with the few metres of basal conglomerates and dolomites reported (Oswald 1955) only about 15 km to the north-west of Big Dog in the Ballyshannon region, at up to 50 m above sea-level. Here these basal Carboniferous rocks are of low Viséan age (Sheridan 1972). Thus over about 15 km there is a fall in the base of the Carboniferous of nearly 2000 m and a corresponding increase in its age. In addition, the underlying strata in the Ballyshannon region are metamorphosed Moinian schists, whilst to the south-east, although not proven in the Big Dog bore, folded Lower Devonian and Old Red Sandstone rocks underlie the Carboniferous. Sheridan (1972) discussed the possibility of this apparently steep palaeoslope being the result of penecontemporaneous fault movement but concluded that block faulting of an early Viséan age resulted in the removal of the Tournaisian and Old Red Sandstones from the Ballyshannon horst region. It is becoming increasingly clear that some rocks in the British Isles much resembling the upper Old Red Sandstone (see Gayer *et al.* 1973) are really Tournaisian in age; these arenaceous transitional beds may be dated using spores, as has been done in Belgium. The lithologies of the lowest 600 m or so of the Big Dog bore indicate shallow marine and lagoonal conditions. Taken together, these two points lead to the conclusion that probably there was a long mid- and lower Tournaisian history of slow deposition in the area while the Old Red Sandstone lands gradually subsided. Periodically the lands were flooded with marine waters which led to the development of evaporites. Tournaisian subsidence to the south-east of the Highland Boundary Fault line was probably greater than that in the Ballyshannon region so that only thin, very condensed, erosional and regressive sediments older than V1b remain on this horst.

These, as yet poorly known, subsurface beds correlate with at least the upper part of Ramsbottom's (1973) First Major Cycle and may also include rocks within at least the lower part of his Cycle Two, which are of V1a age on the Belgian scale.

Viséan. Major Cycle Three, starting probably at the base of V1b (late C_2 of the coral-brachiopod zonation), spread northwards into north-west Ireland as an important transgression and resulted in the deposition of the Ballyshannon Limestone. The regressive phase is represented by the Lower Bundoran Shale and the sporadically-developed Dowra Sandstone.

The Ballyshannon Limestone strikes east–west from the type area into Co. Fermanagh, bordering the Moinian basement to the north, and in the region of Lower Lough Erne is repeated on the south shore by faulting. In our area this repeated section is exposed and extensively quarried from near Enniskillen in a north-westerly direction to Blaney. Being a relatively impervious and hard limestone it forms part of the south-west shore of the lake. Fine examples of *Delepinea destinezi* (Vaughan) have been described from the exposures on the north shore of the Lough (Pettigo Limestone of Simpson 1953) and date these rocks as from the C_2S_1 Zone.

The Dowra Sandstone was recorded from the Big Dog bore and, if correlated with the base of the Clonelly Sandstone of the Omagh basin (Simpson 1955), it represents a southerly extension of the conglomeratic and deltaic sandstones which spread from the north. Surface exposures of pre-upper Viséan (V3) sandstones are uncommon in west Fermanagh and the separation of those attributed to the Dowra Sandstone and those correlated with the Mullaghmore (Derrygonnelly or Macnean) Sandstone is difficult. Both may contribute to the topographical ridge extending from near Enniskillen to Derrygonnelly, where the undoubtedly younger of the two is exposed, marking the upper regressive phase of Cycle Four. At Derrygonnelly this sandstone is well-sorted and contains about 50% calcite cement; it is between 100 and 200 m thick. In addition to the microfauna reported by Sheridan (1972) a transported macrofauna of bryozoans, brachiopods, coiled cephalopods and bivalves has been collected from temporary excavations which show the deposit to be fully marine. The environment in this area was probably a delta front, while coarser, less calcareous near-shore sands accumulated to the north. These sands, like the older Dowra Sandstone, were derived from the north and north-west, principally from the Moine and Dalradian areas of Co. Donegal. They extend from Donegal (the Mountcharles Sandstone), *via* the Mullaghmore type area on the Sligo coast, in a wide belt (known principally from bore-hole evidence) to the east, where they re-appear in the Dungannon region.

The shales below and above the Mullaghmore Sandstone, the Upper Bundoran and Benbulben Shales respectively, are poorly exposed in west Fermanagh. They occupy low boggy ground, commonly covered by glacial drift and alluvium.

The Dartry Group

The shales and argillaceous limestones of the Benbulben Shale Formation represent the return to open marine conditions at the start of Major Cycle Five (V3b). This is an important cycle in north-western Ireland, its rocks are varied and in west Fermanagh increasingly well exposed. No junction between the Mullaghmore Sandstone (Derrygonnelly Sandstone locally) and Benbulben Shale can be seen in west Fermanagh and the shale is known only from small stream sections, principally in the Magho area, close to Lough Erne. It is a blue-grey muddy shale containing sparse thin limestones and bands of concretions, some of which contain a rich fauna of marine invertebrates.

The gradational passage from the Benbulben Shale to the Glencar Limestone can be seen in the Magho area and from this point on a complete succession can be built up from a number of localities.

The Glencar Limestone succession in Fermanagh is very similar to that in Co. Sligo, consisting of approximately equal proportions of interbedded argillaceous limestones and shales, as described by Schwarzacher (1964) from the type area. These rocks are commonly very fossiliferous, especially in their upper sections, containing abundant brachiopods, bryozoans, crinoids and (more locally) corals, and it is from the highest beds of this Formation that finely silicified brachiopods and bryozoans have been described by Brunton (1966*a*, *b*, 1968) and Tavener-Smith (1965, 1973). Palaeocurrent study indicates that clastic sediment was probably all derived from the north and north-west, with open shallow seas extending to the south, whilst in the Sligo area the Ox Mountains appear to have contributed sediment along with that from the Donegal region (Schwarzacher 1968).

The full thickness of the Glencar Limestone is estimated at about 150 m, and towards the top the proportion of limestone to shale increases with thin beds of 'reefal' calcilutite or limestone conglomerates (Schwarzacher 1961) being found in areas where lime-mud mounds developed in the overlying Dartry Limestone.

The Glencar Limestone to Dartry Limestone junction varies in nature between those areas of regularly-bedded Dartry Limestone, such as the Magho region in the north-west of our area, and those localities in which lime-mud mounds developed at an early date, such as the Killydrum region. (Following Wilson's (1975) synthesis of carbonate facies the term 'lime-mud mound' is used here for those facies commonly in the past called 'reefs'. For the sake of brevity the term 'reef' is used on the Figures.) In the Magho area there is a gradational change over some metres of rock showing a reduction in the shale content and the development of relatively thick (5–20 cm) dark limestones containing nodular or tabular cherts. Unlike the Dartry Limestone of the type area, in Co. Sligo, thin shale partings persist almost throughout the formation in west Fermanagh. The junction in areas of lime-mud mounds is commonly abrupt, with the sole of the mud mound overlying crinoid-rich uppermost Glencar rocks. In other places the development of lime-mud mounds was delayed so that their bases are within the standard bedded Dartry Limestone facies. The overall picture during the time of deposition of the upper Glencar and Dartry limestones is of a reduction in the mud content and establishment of clearer-water shelf-margin marine conditions. This period represents the most fully marine phase of Major Cycle Five, and the development of mud mounds indicates a shallowing of marine conditions, leading to the regressive phase and spread of deltaic Glenade Sandstone which terminated this major cycle.

In west Fermanagh there are strong lateral facies changes in the Dartry Limestone, from regularly-bedded chert-bearing limestones to lime-mud mounds (Fig. 3) which influence the present upland regions, commonly producing a knoll-like topography. Faulting between Magho and Killydrum, associated with the Highland Boundary Fault zone, partially obscures this facies change, but it also provides fine sections through some mud mound complexes.

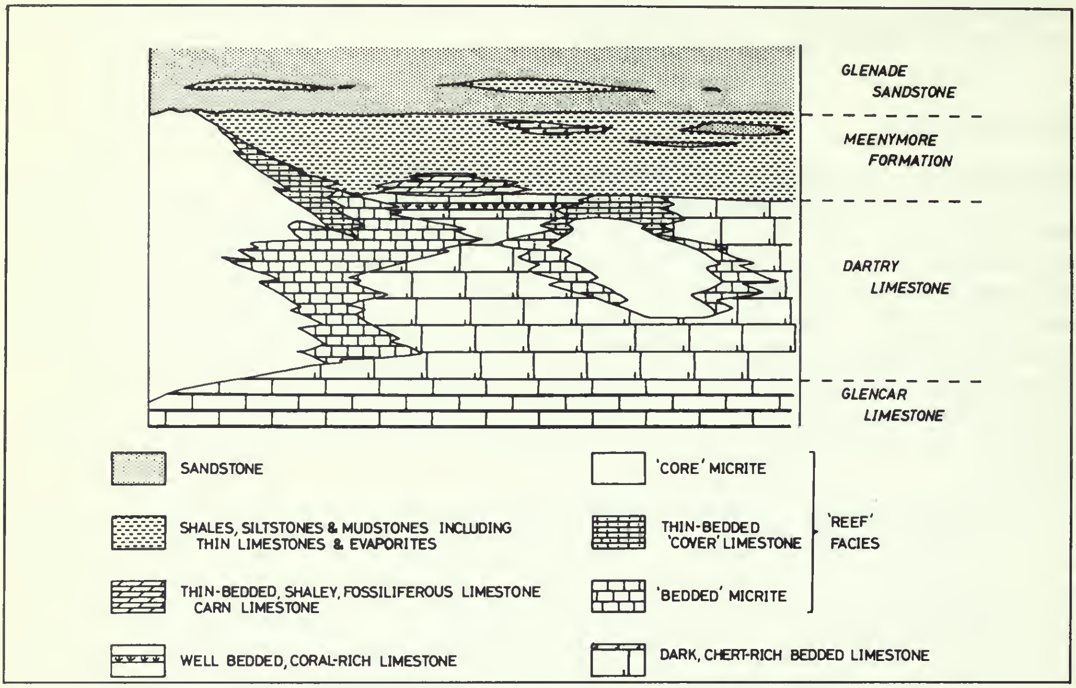

GLENADE SANDSTONE
MEENYMORE FORMATION
DARTRY LIMESTONE
GLENCAR LIMESTONE
SANDSTONE
SHALES, SILTSTONES & MUDSTONES INCLUDING THIN LIMESTONES & EVAPORITES
THIN-BEDDED, SHALEY, FOSSILIFEROUS LIMESTONE CARN LIMESTONE
WELL BEDDED, CORAL-RICH LIMESTONE
'CORE' MICRITE
THIN-BEDDED 'COVER' LIMESTONE
'BEDDED' MICRITE
'REEF' FACIES
DARK, CHERT-RICH BEDDED LIMESTONE

Fig. 3. Diagrammatic representation of the principal facies associated with lime-mud mounds occurring in the highlands of west Fermanagh. Lateral and vertical dimensions are not to scale.

The lime-mud mounds in this area are like those fully described by Schwarzacher (1961) from counties Sligo and Leitrim and resemble those from northern England (Black 1954, etc.) or, to some extent, the type Waulsort 'reefs' of Belgium, as well as the Waulsortian facies of south and central Ireland. Wilson (1975) widely discussed the various lithologies which have in the past been termed 'reefs', 'bioherms', etc. His general term for all such lithologies, 'carbonate buildup', was subdivided on compositional criteria to include his terms 'lime mud mounds' and 'linear mud accumulations', which were defined as lithologies in which 'lime mud matrix dominates other constituents such as organic boundstone and bioclastic debris. Such buildups are commonly perceived to accumulate both through hydrodynamic processes and *in situ* organic production.' It is this definition which most closely fits the facies previously termed 'reef complex' in the Dinantian of north-west Ireland. Within the nine facies belts recognized by Wilson (1975), belt five is mostly of organic reefs on platform margins, but includes non-organic reefs. Wilson distinguishes three types of facies. Type I is carbonate-mud and organic detritus accumulations; Type II is a margin slope, knoll reef, facies combining organic frame builders with lime-mud accumulations, and Type III is the facies of true frame-constructed organic reefs on platform rims. The Fermanagh carbonate buildup facies fall principally into Type I, but grade rarely into the Type II situation as the Dinantian sea became shallower.

The Fermanagh mud mound complexes include several lithologies, each of which may grade into the others laterally or vertically (Fig. 3). These include the following.

1. Massive core micrite in which bedding is absent, apart from occasional erosional planes. The rock is a light-coloured calcilutite containing a few cavities filled by sparry calcite. Fossils are rare.

2. Bedded micrite, which in hand specimen is virtually indistinguishable from the core micrite, contrasts in the field by being well bedded and commonly weathered to a rubbly surface. It forms the main mass of small complexes and grades from the tops and flanks of larger mud mounds having a true core, from which it dips at angles of up to about 40°. In these bedded micrites fossils are locally abundant, sometimes associated with the spar-filled cavities contributing to the rubbly weathered appearance. Elsewhere bryozoan fronds are preferentially aligned more or less parallel to the bedding planes (see Schwarzacher 1961).

3. Bedded cover limestones grade from the bedded micrite and, because the cavities are smaller and the individual beds thinner, their weathered surfaces erode to a fine rubbly appearance with individual pieces about 2 cm across. As the name suggests, these limestones are found above major mud mounds and are normally extremely rich (up to about 40%) in the debris of crinoids and blastoids. These organisms probably flourished in the shallow water at the tops of the mounds, locally in an environment more like the knoll reefs (Type II) of Wilson (1975). The limestone usually consists of broken shell debris producing a coarse lime sand.

The relationships of adjacent mud mounds one to another and to their surrounding chert-rich bedded limestone is one of lateral as well as upward sedimentation through time (Fig. 3). In this way adjacent mounds coalesced or overlapped and the height, or time, to which any one complex developed varied. Thus some mounds are overlain by several metres of normally-bedded Dartry Limestone with chert, though lacking shale partings, deposited before the first shale member of the Meenymore Formation. In other places, flanking the highest mounds, a few metres of well-bedded clean limestones, some of which contain widespread colonies of *Lithostrotion* corals, were deposited prior to the return of the chert-bearing limestone facies. These coral-rich limestones, near the top of the Dartry Limestone formation, indicate a short period of shallow-water clear marine conditions before the deposition of the very argillaceous, but fossiliferous, limestones and shales locally known as Carn Limestones. These represent the start of the strongly regressive phase towards the end of the Fifth Major Cycle and locally they are the basal rocks of the Meenymore Formation. Elsewhere in west Fermanagh mud mound cover limestones are followed directly by Meenymore shales or by even younger Glenade Sandstone.

The Leitrim Group

The Leitrim Group includes all the formations overlying the Dartry Limestone, up to and including the Namurian Dergvone Shale. Of these formations only the Glenade Sandstone is well exposed. The best outcrops of the Meenymore Formation are found near the town of Garrison, where streams have cut through the peat- and drift-covered slopes above Lough Melvin. The Formations younger than the Glenade Sandstone are restricted to the area around the Doagh Syncline, which has been described by Brandon (1972).

The lowest formation of the Leitrim Group is the Meenymore Formation, first described by Brandon (1972), with its type section in Co. Leitrim. This formation is found all over north-west Ireland (Brandon 1977) and its base is always sharply defined. It attains a maximum thickness of about 100 m in the Glen Syncline and is missing over some of the 'reef' areas of the underlying Dartry Limestone. The formation may be divided into lower and upper parts by the main marker horizon, the prominent calcareous Quarry Sandstone Member. The lower part of the formation is mainly composed of shaly limestones and mudstone, while the sequence above the Quarry Sandstone Member is characterized by the presence of laminated carbonates. In both the upper and lower parts evaporites are found.

As the Meenymore Formation is extremely variable in thickness and lithology, it is ideal for detailed sedimentological study, but this variation also makes it difficult to correlate the exposures.

A goniatite–nuculid fauna from Glennasheevar contains *Bollandoceras* indicative of the B_2 subzone (V3b). This implies that the Glenade Sandstone above is of B_2 or P_{1a} age, since the Bellavally Formation contains a P_{1b} fauna.

The main lithologies of the Meenymore Formation may be summarized as follows.

(a) Calcareous sandstones and siltstones.
(b) Shaly and sandy limestones.
(c) Laminated micrites, siltstones and dolomicrites (collectively known as laminated carbonates).
(d) Limestones containing pseudomorphs after evaporite minerals.
(e) Shales, mudstones and siltstones. Fissile, pyritic, micaceous and varying in colour.

The most characteristic lithologies are the laminated carbonates, and their presence suggests that the formation was deposited in a sabkha-like environment (Gardiner & Mason 1974), a conclusion which was supported by the discovery of evaporites.

The laminated carbonates can be subdivided into three main types.

(a) Planar laminated carbonates; dolomite content variable, usually unfossiliferous.
(b) Brecciated laminated carbonates; dedolomitized or with high dolomite content. Occasional fossil fragments.
(c) Laminated carbonates; dolomitic, containing trace fossils.

These rocks were deposited in a peritidal environment, as they all exhibit algal fabrics.

The planar laminated carbonates consist of thin (5–15 cm) bands of flaggy carbonate, with a conspicuous lamination on the weathered surface. These laminae, which are parallel to bedding, are composed of very thin (0·1–1·0 mm thick), alternating layers of dolomite and calcite. It is likely that they were formed as described by Gebelein & Hoffman (1973), who claimed that there is sufficient magnesium complexed into organic algal sheath material to form dolomite during diagenesis. Scanning electron micrographs of the laminated rock types show the dolomite to be undoubtedly of secondary origin. Finely laminated lithologies like these are common in the geological column (Sander 1936; Sarin 1962; Laporte 1967; Hoffman 1970).

The brecciated laminated carbonates were formed by subaerial desiccation of algal mats under arid conditions. The broken fragments are polygonal, averaging about 1 cm² in area. The polygonal pieces are of a lighter buff colour than the greyish sediment-filled cracks separating them. Sections polished at right angles to bedding show the fragments of algal material to vary in thickness from 0·5 mm to 5·0 mm, whilst the sediment layers are 1·0 mm or less in thickness. In thin section these rocks show the following features.

(a) Pseudomorphs of calcite after dolomite.
(b) Palimpsest textures, with rhombic zones of ferric oxides remaining as ghosts within a new generation of calcite.
(c) Possible dolomite inclusions within the calcite pseudomorphs (seen with the scanning electron microscope only).

These features fulfil criteria established by Shearman *et al.* (1961) to define dedolomitized lithologies. The mechanism offered to explain this phenomenon utilizes the reversible reaction

$$2CaCO_3 + MgSO_4 \rightleftharpoons CaCO_3MgCO_3 + CaSO_4,$$

thus requiring a gypsiferous solution to effect dedolomitization. This could easily have been derived from the various evaporites within the Meenymore sequence, and the soluble magnesium sulphate produced by the reaction would be removed by rainfall. Gypsum was found at Killybeg crystallized along bedding planes and joint surfaces as a Recent deposit. Dedolomitization is essentially a near-surface or surface reaction.

The remaining laminated carbonate contains tube-like trace fossils, which are often concentrated on bedding surfaces. A detailed study of these (Mason in press) has led to the conclusion that they were the fossil remains of polychaete worm tubes. They were probably made by a small sedentary polychaete resembling the Recent species *Sabella microphthalma* which Neumann *et al.* (1970) describe as a common faunal element of subtidal algal mats of the Bahamas. These tubes exhibit a preferred orientation, and it is possible that they were sufficiently rigid to withstand

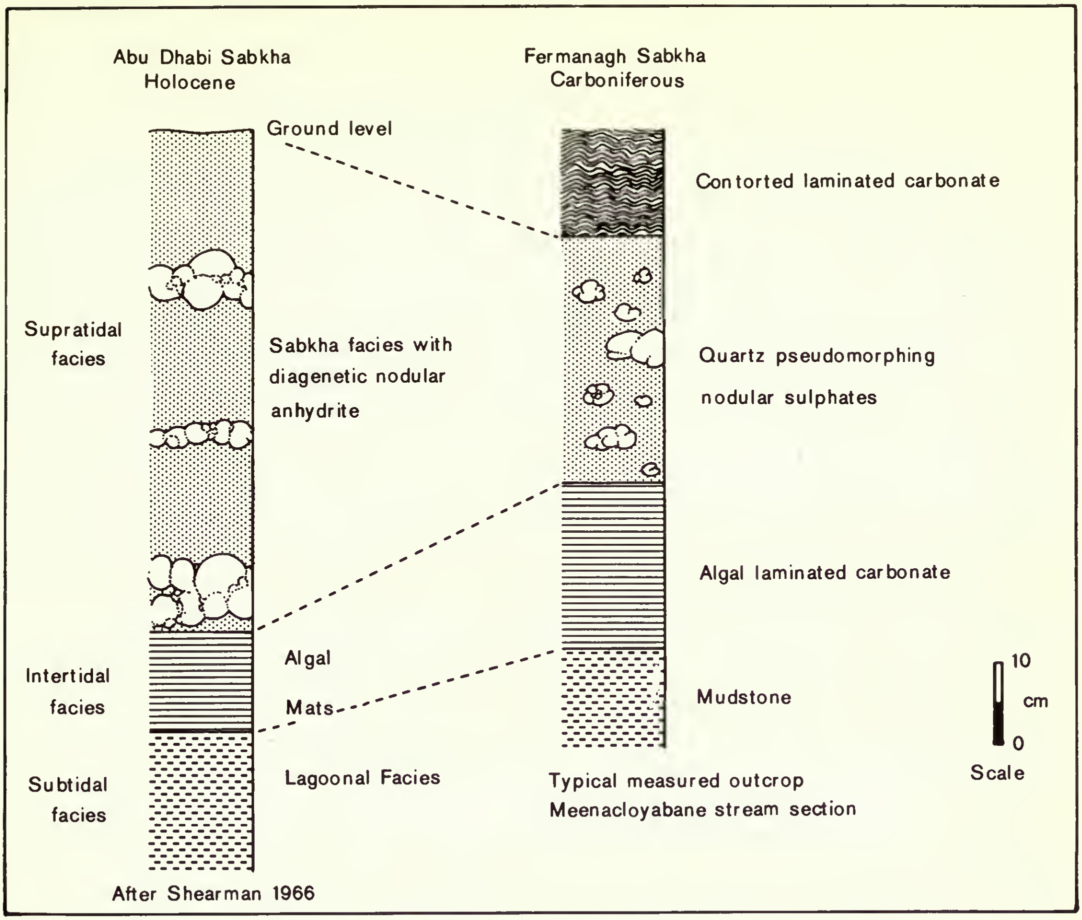
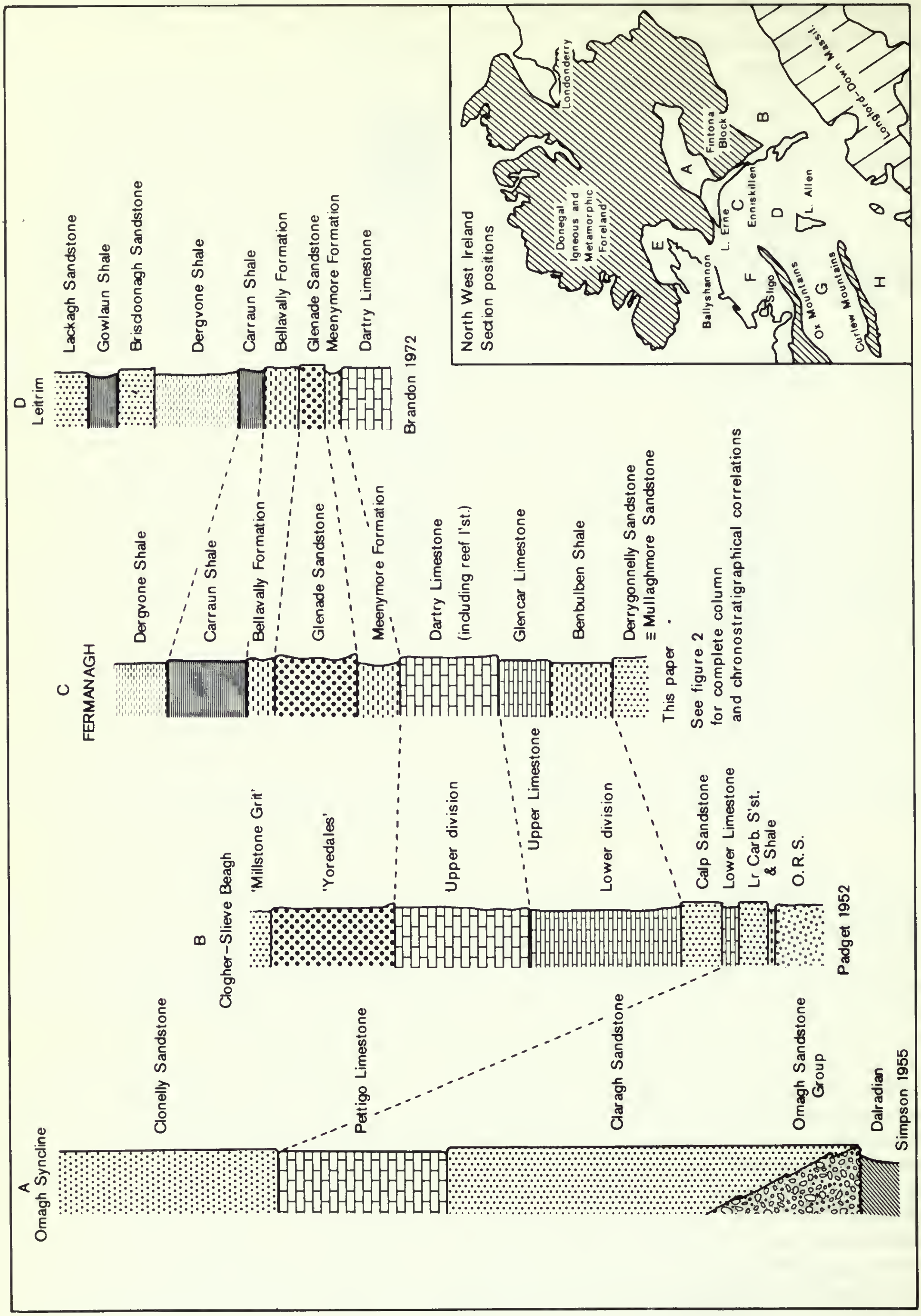

Abu Dhabi Sabkha
Holocene
Fermanagh Sabkha
Carboniferous
Ground level
Contorted laminated carbonate
Supratidal facies
Sabkha facies with diagenetic nodular anhydrite
Quartz pseudomorphing nodular sulphates
Algal laminated carbonate
Intertidal facies
Algal Mats
Mudstone
10
cm
0
Scale
Subtidal facies
Lagoonal Facies
Typical measured outcrop
Meenacloyabane stream section
After Shearman 1966

Fig. 4. A typical sabkha cycle from Abu Dhabi and the Carboniferous analogue from a section in Co. Fermanagh.

transportation and reworking by currents. The diagenetic history of this rock is one of progressive dolomitization.

Many of the laminated carbonates are contorted and folded, suggesting that they were still plastic when deformed. Examination of the different types of distortion suggested kinship with some of the algal zones described by Kendall & Skipwith (1968) from the Persian Gulf. One algal limestone from Shroneallappa contains rounded colonies of *Ortonella furcata* which closely resemble the algal colonies of the cinder zone (Kendall & Skipwith 1968).

If it is to be accepted that there is a close comparison between the west Fermanagh Meenymore Formation and the sedimentary regime of the present Persian Gulf, supporting evidence is required. In the Persian Gulf Shearman (1966) recognized a sabkha cycle of deposition comprising firstly sandy carbonate with sulphate nodules, then algal mats, and finally lagoonal facies. Similar cycles occur in the Meenymore Formation (Fig. 4), except that those of the Viséan have been altered during diagenesis. A diagenetic history may be constructed to show the sequence of replacement. The main difference between the Carboniferous and Recent sediments is the Carboniferous lack of calcium sulphate, most of which has been replaced diagenetically by celestite, chalcedonic silica (lutecite) and megaquartz. Lens-shaped pseudomorphs after gypsum, and megaquartz replacement of anhydrite nodules, are also recorded. It appears that the depositional environment during Meenymore times resembled the coastal sabkhas of the Persian Gulf at the present time.


A
Omagh Syncline
Clonelly Sandstone
Pettigo Limestone
Claragh Sandstone
Omagh Sandstone Group
Dalradian
Simpson 1955
B
Clogher–Slieve Beagh
'Millstone Grit'
'Yoredales'
Upper division
Upper Limestone
Lower division
Calp Sandstone
Lower Limestone
Lr Carb. S'st. & Shale
O.R.S.
Padget 1952
C
FERMANAGH
Dergvone Shale
Carraun Shale
Bellavally Formation
Glenade Sandstone
Meenymore Formation
Dartry Limestone
(including reef l'st.)
Glencar Limestone
Benbulben Shale
Derrygonnelly Sandstone
≡ Mullaghmore Sandstone
This paper
See figure 2
for complete column
and chronostratigraphical correlations
D
Leitrim
Lackagh Sandstone
Gowlaun Shale
Briscloonagh Sandstone
Dergvone Shale
Carraun Shale
Bellavally Formation
Glenade Sandstone
Meenymore Formation
Dartry Limestone
Brandon 1972
North West Ireland
Section positions
Londonderry
Donegal Igneous and Metamorphic 'Foreland'
Fintona Block
Longford–Down Massif
A
B
C
D
E
F
G
H
Enniskillen
L. Erne
L. Allen
Ballyshannon
Sligo
Ox Mountains
Curlew Mountains

The Glenade Sandstone is exposed as a series of prominent escarpments forming much of the high ground in the area. Sandstones are interbedded with thin shales whose presence may be inferred by the occurrence of shaly clasts in the basal parts of the sandstone outcrops. Some shales seen in a quarry face were pinched into lenses by compaction. Conglomeratic horizons are common near the base of the formation. They contain small (2 cm) shale clasts, well-rounded quartz pebbles (2–3 cm diameter) and coaly debris, thought to have formed *in situ* from drifted plant remains. Some horizons contain numerous unidentifiable plant fragments.

Petrographically the Glenade Sandstone contains *c.* 95% quartz, 4% calcite or dolomite cement and 1% feldspar. The occurrence of two generations of calcite, one of which is limpid and the other darker containing ferric oxide, suggests that an original dolomite cement has been dedolomitized. Rhombic crystals of iron-rich calcite resembling the rhombic ghosts of dolomite crystals occur in the brecciated laminated carbonates. In the type area Oswald (1955) described the Glenade Sandstone as containing up to 50% feldspar. The lower amount of feldspar in the Fermanagh outcrops probably reflects their greater distances from the inferred source areas to the north and north-west.

All the Carboniferous sandstones in Fermanagh thin southwards, and each sandstone in the succession advanced further south than its predecessor. The thickest sandstones in the Leitrim area are of Namurian age (E_2), suggesting that the shoreline was prograding and advanced south with time. The Glenade Sandstone thins from about 200 m in Fermanagh to about 30 m in Leitrim.

Compaction in the Glenade Sandstone, in addition to pinching out the shaly horizons, also produces a characteristic 'wavy' bedding, with 'waves' up to an amplitude of 0·75 m and wavelength 4 m. Most other sedimentary structures are localized. Current bedding readings suggest a northerly source for the sediment.

Large limestone clasts (500 ml) found in the basal part of the formation are thought to be eroded blocks of Dartry Limestone, as the basal Glenade Sandstone rests on mud mound limestone where the Meenymore Formation is attenuated or absent. These contacts are poorly exposed and can be deduced most easily from aerial photographs.

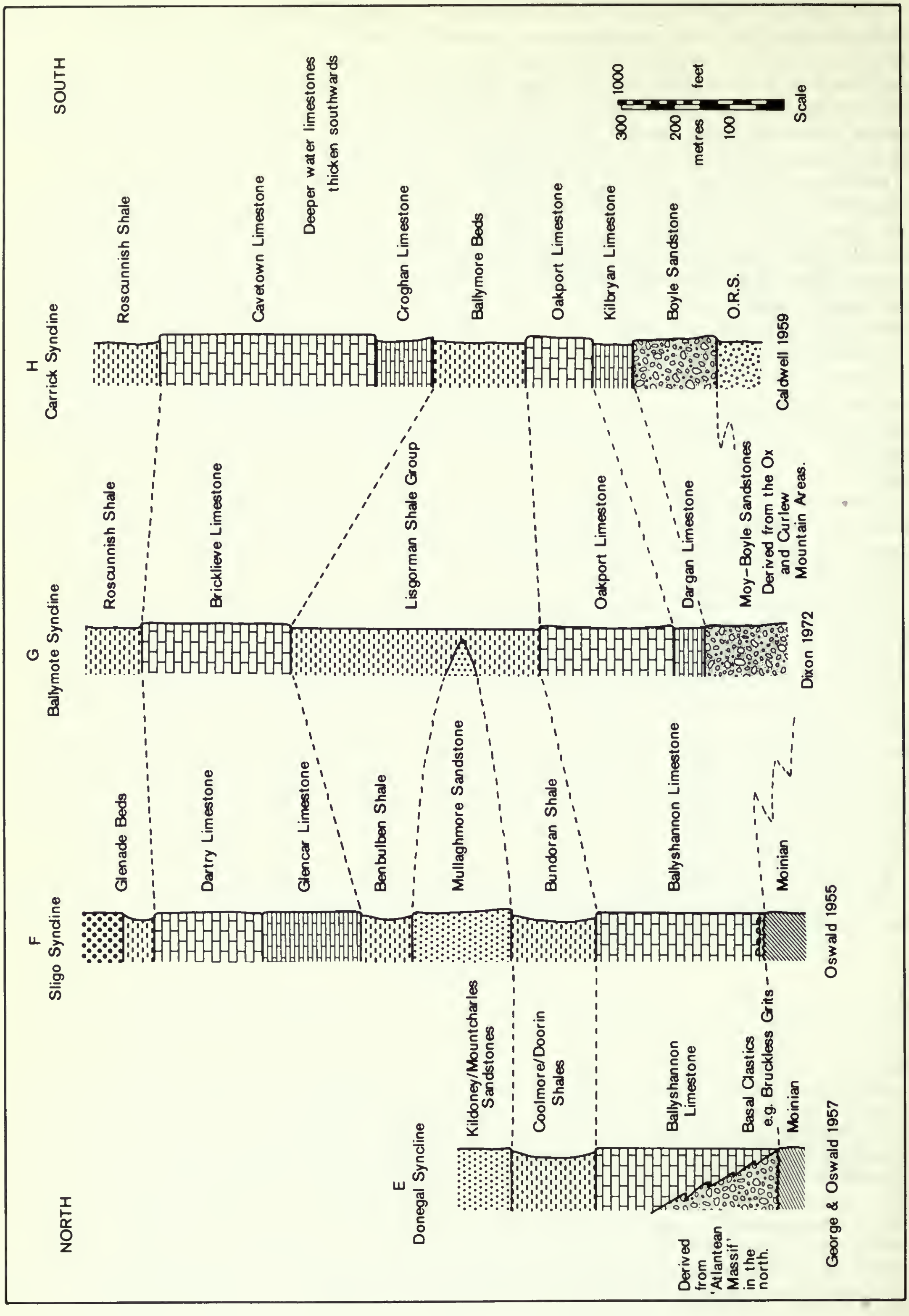
The formations above the Glenade Sandstone are poorly exposed in Fermanagh and crop out only in the Doagh Syncline. This is the most northerly occurrence in Ireland of these strata, the nearest related succession being found in Leitrim. It is only possible to construct the succession up to the Dergvone Shale by mapping the various limestone marker horizons, and by collecting their distinctive faunas (Fig. 2). In west Fermanagh the succession is about twice as thick as that in Leitrim, which reflects the close proximity of Fermanagh to the source of the sediment on the old Carboniferous continent.

Brandon (personal communication) has remarked on the apparent cyclicity of the Carraun Shale (Fig. 2), which is primarily composed of limestone–shale alternations, thus reinforcing Ramsbottom's (1973) views on the minor cyclicity of Major Cycle Six.

Correlations

Age determination and correlation based upon faunas in west Fermanagh is poor, except for

Fig. 5. Generalized stratigraphical sections A–D, based on published work and our own studies, showing major facies changes and their correlations with the formation names derived from Oswald (1955) and Brandon (1972). From left to right the columns represent increasingly southerly positions and are interpreted as being successively further from the Carboniferous landmass to the north. The Clogher-Sliĕve Beagh section (Paget 1952) may be atypical of that basin as a whole. Sheridan (1972) presented data from the Glenoo no. 1 well, drilled a few km south-west of Sliĕve Beagh, which when tabulated provides approximately 2260 m of sediment from near the base of the Dartry Limestone equivalent down to the top of the supposed Old Red Sandstone. This Glenoo succession includes about 250 m of sandstone, which can be correlated with the Mullaghmore Sandstone, and about 1900 m of limestones and thin shales of the Ballyshannon Limestone type. Below this about 1350 m of mixed sandstones, shales, occasional limestones and anhydrites were penetrated which appear similar to those recorded from the base of the Big Dog well in Fermanagh, where they are marked as Basal Clastics in Fig. 2, p. 94.


NORTH
SOUTH
E
Donegal Syncline
F
Sligo Syncline
G
Ballymote Syncline
H
Carrick Syncline
Kildoney/Mountcharles Sandstones
Coolmore/Doorin Shales
Ballyshannon Limestone
Basal Clastics e.g. Bruckless Grits
Moinian
Derived from 'Atlantean Massif' in the north.
George & Oswald 1957
Glenade Beds
Dartry Limestone
Glencar Limestone
Benbulben Shale
Mullaghmore Sandstone
Bundoran Shale
Ballyshannon Limestone
Moinian
Oswald 1955
Roscunnish Shale
Bricklieve Limestone
Lisgorman Shale Group
Oakport Limestone
Dargan Limestone
Moy–Boyle Sandstones
Derived from the Ox and Curlew Mountain Areas.
Dixon 1972
Roscunnish Shale
Cavetown Limestone
Deeper water limestones thicken southwards
Croghan Limestone
Ballymore Beds
Oakport Limestone
Kilbryan Limestone
Boyle Sandstone
O.R.S.
Caldwell 1959
300
200
metres
100
1000
feet
Scale

some of the younger strata. However, some faunas of significance have allowed us to correlate the formations in north-west Ireland (Figs 5, 6) and to suggest the zonal correlations we present in Fig. 2, p. 94. No stratigraphically important faunas have been described from the Ballyshannon Group, although where better exposed in County Sligo Oswald (1955) records *Michelina megastoma* (Phillips) (= *M. grandis*) and *Delepinea destinezi* (Vaughan) in the Ballyshannon Limestone itself. These are typical C_2S_1 or Cycle Three fossils. *D. destinezi* is also known from the equivalent limestone exposures on the north shore of Lower Lough Erne near Kesh (Simpson 1953). In this region Simpson (1955) reported *Davidsonina carbonaria* (M'Coy) from sandstone (? Mullaghmore Sandstone) above the local Ballyshannon Limestone and this would correlate with the S_2 or Cycle Four; however, this record has not been verified.

Only in the uppermost Benbulben Shale are exposures good and fossils plentiful. Unfortunately, diagnostic macrofossils remain poorly known despite the excellence of silicified bryozoans and brachiopods described from the Glencar/Dartry Limestone junction. These faunas have been assigned by Tavener-Smith and Brunton to the D_1 Zone, or Cycle Five. The characteristic brachiopods of this Cycle, *Davidsonina septosa* (Phillips) and *Daviesiella llangollensis* (Davidson), found in central and northern England, appear to be missing from north-west Ireland. This absence may result from palaeoenvironmental differences between the pale bioclastic limestones low in the D_1 Zone, where they are normally found, and the contemporaneous muddy limestones of north-west Ireland.

Of the abundant silicified brachiopod species collected from Co. Fermanagh, *Plicatifera plicatilis* (J. de C. Sowerby), *Overtonia fimbriata* (J. de C. Sowerby), *Krotovia spinulosa* (J. Sowerby), *Productina margaritacea* (Phillips) and eomarginiferids such as *Eomarginifera trispina* Brunton are normally typical of D_1 limestones in Britain. Unfortunately, foraminifera are rare in most of these limestones and have not yet been studied in detail. However, small samples of Glencar and Dartry Limestones kindly examined by Professor R. Conil suggest to him (*in lit.* February 1975) a high V2b to V3a age for a low Glencar Limestone sample. A V3a age for this sample is equivalent to S_2 Zone and would thus extend Cycle Four of Ramsbottom (1973) to the base of the Glencar Limestone. From the overlying Leitrim Group shales, good P age goniatites (including *Goniatites striatus* (J. Sowerby) and *G. falcatus* Roemer from the Bellavally Formation) have been collected, so the exact age of the Dartry Group remains somewhat equivocal, but it must broadly coincide with the whole of the D_1 Zone or Cycle Five.

The base of the Namurian is marked by the occurrence of *Cravenoceras* cf. *leion* Bisat and *Eumorphoceras* sp. in the Dergvone Shale from the Doagh outlier. In addition, Brandon (1972) records *Eumorphoceras* cf. *rota* Horn and *E.* cf. *medusa* Yates from these shales, which are the youngest Carboniferous rocks in west Fermanagh.

Discussion

The depositional environments of the west Fermanagh Lower Carboniferous strata may be reconstructed by studying the fauna and lithologies. The sedimentary regime varied from shelf carbonates and shales to deltaic sandstones and coastal sabkhas, and the recognition of Major Cycles Three to Six demonstrates the value of this approach to broad stratigraphic correlation. If this cyclicity is to be of more general help in correlation it is necessary to consider the gross aspects of various Carboniferous successions in the northern hemisphere.

Fig. 6. Generalized stratigraphical sections E–H from areas as indicated in Fig. 5, based on published work, showing major facies changes and their correlations with the formation names derived from Oswald (1955) and Brandon (1972). From left to right the columns represent increasingly southerly positions and are interpreted as being successively further from the Carboniferous landmass to the north, and follow on from A to D (Fig. 5). In the Donegal syncline (George & Oswald 1957) there is considerable facies variation; in the northern parts of the area great thicknesses (over 800 m) of grits and conglomerates were recorded. This correlates with the thick pre-Clonelly Sandstone sequence of the Omagh syncline (Simpson 1955) shown in Fig. 5, A. The Highland Boundary Fault zone passes between sections F and G, affecting the pre-Carboniferous basement rocks as it does in west Fermanagh.

The map prepared by Smith *et al.* (1973) shows that the areas in which Lower Carboniferous sediments were laid down are now fragmented by continental drift, with some pieces now separated by the North Atlantic Ocean. As eastern Canada and Ireland were formerly much closer, one would expect to find evidence of Viséan evaporites and supratidal deposits in the Canadian succession. Schenk (1967), working on the Windsor Group of the Canadian Maritime Provinces, described lithologies which were 'almost identical' to the strand-line carbonates of the present Persian Gulf, Bahamas, Florida Bay and South Australia. He described two peritidal lithosomes, together forming the Macumber Formation, thought to be of Viséan age, and this formation may be closely related to the Irish Meenymore Formation.

Concerning the sequence underlying the Fermanagh Viséan succession, Belt *et al.* (1967) correlated the 'cementstone' facies of eastern Canada, Northern Ireland (Cultra) and the midland valley of Scotland. Recent work on the Irish fauna suggests that the 'cementstones' are of Middle Tournaisian age (Brandon, personal communication). Samples from this succession contain calcitized and dolomitized enterolithic structures similar to those described as calcitized anhydrite by Shearman & Fuller (1969) from the Devonian of Canada. It seems that during the Tournaisian there was an evaporitic interlude, and the successions in eastern Canada, Ireland and Scotland are again remarkably similar. Carboniferous evaporites are also known from the Middle Carboniferous of Svalbard (Spitzbergen) (Holliday 1966), the Permo-Carboniferous of Bjørnøya, Svalbard (Folk & Siedlecka 1974) and the Lower Carboniferous of Alaska (Armstrong 1970); it is likely that other occurrences remain to be discovered and described in Russia and North America.

Green (1961) concluded that the distribution of evaporites was limited to those areas falling between latitudes 45° N and 45° S. The British Isles, and probably Svalbard, would have been within these latitudes during Lower Carboniferous times (Smith *et al.* 1973), it is suggested that there is sufficient similarity between the British and Irish successions, and that of eastern Canada and possibly Svalbard, to permit them to be correlated on the basis of the over-all sequence.

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The Ordovician trilobite faunas of the Builth Llandrindod Inlier, central Wales. Part III

C. P. Hughes

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The Ordovician trilobite faunas of the Builth–Llandrindod Inlier, central Wales. Part III

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Synopsis

This paper, third in a series describing the Ordovician trilobite faunas of the Builth–Llandrindod inlier, describes representatives of the families Cyclopygidae, Asaphidae, Nileidae, Odontopleuridae and Proetidae. *Emmrichops* ? *extensus*, *Pricyclopyge wattisoni*, *Nobiliasaphus powysensis*, *Barrandia expansa* *Barrandia ultima* and *Homalopteon murchisoni* are described as new. A lectotype for *Ogygiocarella angustissima* (Salter) is selected.

Terminology

The terminology used is that of Harrington, Moore & Stubblefield (*in* Moore 1959) with, in addition, a few terms introduced since that date and two proposed here. The new terms introduced by Marek (1961) for the description of cyclopygids have not been adopted as the standard terms in use are believed adequate. Richter & Richter's (1940) 'greek letter' terminology for the path of the facial suture is used in the definition of some of the measurements taken on asaphids and nileids.

The following new terms are proposed:

PARATHORACIC SEGMENT — applied to the region of the transitory pygidium having the form of a thoracic segment but still fused into the pygidial exoskeleton (see *Barrandia* and *Homalopteon*).

YOUNG HOLASPIS — applied to individuals having the full number of thoracic segments but not possessing all other holaspid characters. It is preferred to 'meraspis degree 8' (as applied to asaphids) of Whittard (1964 : 260) since the term meraspis excludes forms possessing the adult number of thoracic segments.

The following terms not listed in Moore (1959) are also used:

PARADOUBLURAL LINE — applied to the line on the dorsal surface of the exoskeleton directly above the inner margin of the doublure (Henningsmoen 1960 : 210).

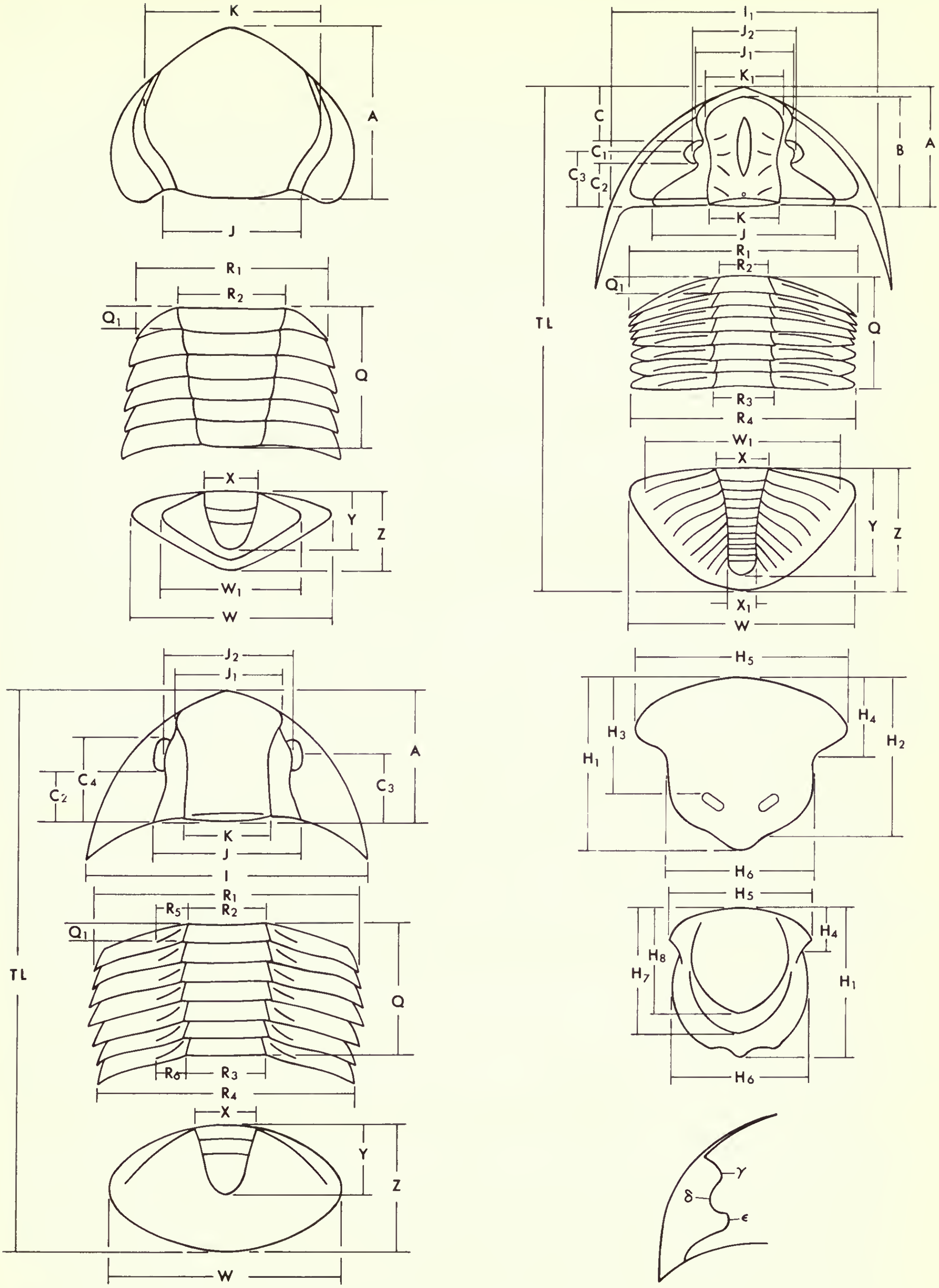
POSTERIOR INDENTATION — applied to the small indentation in the posterior margin of the transitory pygidium in asaphids (Henningsmoen 1960 : 230). As this structure is present in holaspides of certain asaphids (Henningsmoen 1960 : 220; pl. 1, figs 1, 2) this term is preferred to 'larval notch' (Osmolska 1962 : 57).

Definition of measurements

As in earlier parts of this study (Hughes 1969, 1971), the single orientation method of measurements proposed by Shaw (1957) has been followed. In those measurements involving distances between, or to, furrows, the measurements have been taken from the deepest (dorsoventrally) point in the furrow. All measurements are taken from internal moulds except where specifically stated to the contrary. Measurements shown as estimated indicate that measurement was not possible using both defined end points. In width measurements estimates were obtained by the doubling of measurements taken to the sagittal line from one defined end point; in length measurements an estimation was made of the position of one end point by projecting exsagittal features onto the sagittal line. Measurements given to two decimal places are rounded to the nearest 0·05 mm.

Definitions of measurements (see Fig. 1):

A	maximum cephalic length – measured in sagittal line.
B	glabellar length – measured in sagittal line between anterior of glabella and posterior margin of occipital ring (asaphids only herein).
C	prepalpebral length – distance between anterior of cephalon and γ of facial suture, as projected onto sagittal line (asaphids only herein).
C_1	palpebral length – distance between γ and ε of facial suture, as projected onto sagittal line (asaphids only herein).
C_2	postpalpebral length – distance between ε of facial suture and posterior cephalic margin, as projected onto sagittal line.


K
A
J
R_1
R_2
Q_1
Q
X
Y
Z
W_1
W
J_2
J_1
A
C_4
C_2
C_3
K
J
I
R_1
R_5
R_2
Q_1
TL
Q
R_6
R_3
R_4
X
Y
Z
W
I_1
J_2
J_1
K_1
C
C_1
C_3
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B
A
K
J
R_1
R_2
Q_1
TL
Q
R_3
R_4
W_1
X
Y
Z
X_1
W
H_5
H_3
H_4
H_2
H_1
H_6
H_5
H_4
H_8
H_7
H_1
H_6
γ
δ
ϵ

Fig. 1. Diagram showing measurements taken on cyclopygids, ogygids and nileids; also hypostomata and sutural terminology.

C_3	midpalpebral length – distance between δ of facial suture and posterior cephalic margin, as projected onto sagittal line.
I	maximum cephalic width – measured in a transverse direction (nileids only herein).
I_1	cephalic width – measured in a transverse direction along line of posterior cephalic margin (asaphids only herein).
J	posterior cranidial width – measured in a transverse direction along posterior cephalic margin.
J_1	maximum anterior cranidial width – measured in a transverse direction.
J_2	midcranidial width – measured in a transverse direction between δ of facial suture.
K	maximum glabellar width – measured in a transverse direction between axial furrows.
K_1	posterior glabellar width – measured in a transverse direction between axial furrows, along posterior cephalic margin.
K_2	maximum anterior glabellar width – measured in a transverse direction (asaphids only herein).
Q	thoracic length – measured in an exsagittal line between anterior margin of anterior thoracic segment and posterior margin of posterior thoracic segment.
Q_1	axial length of anterior thoracic segment – measured in sagittal line between anterior and posterior margins of anterior thoracic segment.
R_1	anterior thoracic width – measured in a transverse direction between lateral extremities of anterior thoracic segment.
R_2	anterior thoracic axial width – measured in a transverse direction between axial furrows, along anterior margin of anterior thoracic segment.
R_3	posterior thoracic axial width – measured in a transverse direction, between axial furrows along posterior margin of posterior thoracic segment.
R_4	posterior thoracic width – measured in a transverse direction between lateral extremities of posterior thoracic segment.
R_5	measured in a transverse direction between inner doublural margin and axial furrow along anterior thoracic margin (nileids only herein).
R_6	measured in a transverse direction between inner doublural margin and axial furrow along posterior thoracic margin (nileids only herein).
W	maximum pygidial width – measured in a transverse direction.
W_1	intra-marginal pygidial width – measured in a transverse direction between distal extremities of anterior border furrows.
X	anterior pygidial axial width – measured in a transverse direction between axial furrows, along anterior margin.
X_1	posterior pygidial axial width – measured in a transverse direction between axial furrows across posterior of axis (asaphids only herein).
Y	pygidial axial length – measured in sagittal line between articulating furrow and posterior of axis.
Z	pygidial length – measured in sagittal line between articulating furrow and posterior pygidial margin.
T.L.	total length – measured in sagittal line between anterior cephalic margin and posterior pygidial margin.
H_1	hypostomal length – measured in sagittal line between anterior and posterior hypostomal margins.
H_2	distance between anterior hypostomal margin and anterior of median lip as projected onto sagittal line (asaphids only herein).
H_3	distance between anterior hypostomal margin and anterior of maculae, as projected onto sagittal line (asaphids only herein).
H_4	distance between anterior hypostomal margin and posterior extremity of anterior wings, as projected onto sagittal line.
H_5	maximum hypostomal width – measured in a transverse direction.
H_6	posterior hypostomal width – measured in a transverse direction across the maximum width posterior of anterior wings.
H_7	distance between anterior hypostomal margin and posterior border furrow, measured in sagittal line (nileids only herein).
H_8	distance between anterior hypostomal margin and middle furrow, measured in sagittal line (nileids only herein).

Stratigraphy

In earlier parts of this study (Hughes 1969, 1971), the term Llandeilo Series was taken as essentially equivalent to the single assemblage zone of *Glyptograptus teretiusculus*, and beds of low *Nema-*

graptus gracilis Zone age were referred to basal Caradoc Series. Since then, however, Addison (*in* Williams *et al.* 1972 : 35–36) has demonstrated that assemblages indicative of *N. gracilis* Zone age are present in the middle and upper Llandeilo. In this work, therefore, the *G. teretiusculus* Zone is considered to be of lower Llandeilo age and the succeeding beds of basal *N. gracilis* Zone to be of middle and upper Llandeilo age, possibly with the upper horizons being of basal Caradoc age. Thus some beds are assigned an age herein which is different from the usage in my previous papers.

The lithostratigraphical terminology of the region is badly in need of revision; the only available names (e.g. *Glyptograptus teretiusculus* Shales), formalized in Williams *et al.* (1972), though unsatisfactory, are used herein, being the best terms available at present.

Systematic descriptions

Unless otherwise stated, all specimens are in the Department of Palaeontology of the British Museum (Natural History) (registered numbers without prefix, or with prefix I or It). Specimens in other collections are cited as follows:

BU	University of Birmingham
GSM	Geological Survey Museum (Institute of Geological Sciences, London)
NMW	National Museum of Wales, Cardiff
OUM	Museum, Oxford University
SM	Sedgwick Museum, Cambridge
UCW	University College, Aberystwyth

Family **CYCLOPYGIDAE** Raymond, 1925

Genus ***EMMRICHOPS*** Marek, 1961

DIAGNOSIS. Cephalon about twice as wide as long. Eye relatively flat with much of the visual surface directed ventrally. Glabella with three pairs of transversely elongate muscle impressions. Rostral suture not arched downwards. Doublure relatively narrow. Thoracic axis wider than pleural regions; number of thoracic segments unknown. Pygidium unknown.

TYPE SPECIES. *Emmrichops planicephalus* Marek, 1961.

DISTRIBUTION. Dobrotivá Beds (lower Llandeilo) of Czechoslovakia (Marek 1961 : 52) and possibly *Glyptograptus teretiusculus* Shales (lower Llandeilo) of central Wales (herein).

DISCUSSION. Marek (1961) considered the very wide cephalon sufficient to warrant the separation of this genus from *Microparia* Hawle & Corda, 1847, to which he believed it was allied owing to the similarity in cephalic musculature.

Emmrichops ? extensus sp. nov.

(Figs 3, 4, 6, 9)

DIAGNOSIS. Cyclopygid with cranidium much wider than long. Pygidium with concave lateral margins and transversely elongate anterolateral angles.

NAME. 'Dilated'.

TYPE MATERIAL. Holotype, GSM 6142 (Fig. 4), internal mould of pygidium. Paratype, It.2838 (Figs 3, 6, 9), external mould of pygidium and associated internal mould of damaged cranidium.

DIMENSIONS (in mm).	W	X	Y	Z
Holotype	24·7	7·5	6·5	8·4
It.2838	*c.* 14·0	4·0	3·7	5·8

For explanation of symbols see Fig. 1.

TYPE LOCALITY AND HORIZON. The exact locality from which the holotype was collected is uncertain. The specimen is labelled 'Pen Cerrig, Builth' and it is possible that it is from the quarry at the south-western end of Pen-cerig Lake, although collecting at this locality has not yielded further specimens. The paratype is from exposures in the left bank of the stream section east of Bach-y-graig, 40 yd (37 m) upstream of the point where the footpath enters the wood at the western end of the section. If the holotype is from Pen-cerig, then it is from slightly younger beds than those from which the paratype was recovered, though both lie within the *Glyptograptus teretiusculus* Shales of lower Llandeilo age.

Description. The single known cephalon is compressed, cracked and incomplete, but is clearly very much wider than long. It shows no obvious signs of glabellar furrows or nodes, though faint traces of possible muscle scars are present posteriorly. The preserved eye (right) is well developed; possibly not fused anteriorly with left. Lenses hexagonal except for inner median portion where they are modified to be approximately rectangular (Fig. 9).

Thorax unknown.

Pygidium nearly three times as wide as long, subtriangular with anterior margin gently convex forwards and lateral margins markedly concave (Figs 4, 6). Axis occupying nearly one-third of anterior width tapers gently to the posterior, occupies about four-fifths of pygidial length and terminates obtusely before reaching border furrow. Posterior of axis more clearly defined in holotype than in paratype pygidium where it merges into postaxial field. Anteriorly a single well-defined axial ring is developed with, in the holotype, faint traces of three further rings. Pleural field smooth and inflated. Wide, shallow border furrow present laterally and anteriorly, becoming less well defined posteriorly. Doublure narrow, underlies posterolateral border and bears several subparallel terrace lines.

Discussion. The species is here tentatively assigned to *Emmrichops* mainly on the basis of the very wide cephalon. Whilst it is recognized that the unusual outline of the holotype may be due to *post-mortem* deformation, the symmetry of the specimen together with the relatively small amount of cracking or buckling of the specimen argues against tectonic deformation. The lateral margins of the paratype pygidium are not well preserved but appear to be of the same general form as those of the holotype, though possibly with a slightly smaller anterolateral projection. Although the pygidium of *Emmrichops* has not been described, it is likely to be relatively wide and the pygidium described here is not obviously anomalous when compared to the cephalon of the type species. Of other cyclopygid genera in which the pygidium is known, *Pricyclopyge* possibly exhibits the most similarity. However, the rather unusual outline of *E.* ? *extensus* distinguishes it from all known *Pricyclopyge* species.

Genus ***PRICYCLOPYGE*** R. & E. Richter, 1954

Diagnosis. Cephalon larger than pygidium and somewhat wider than long. Glabella with four pairs of muscle scars. Librigena very small. Eye large, highly convex. Rostral suture, if developed, moderately vaulted upwards. Thorax of six segments. Pygidium subtriangular with distinct axis and border.

Type species. *Aeglina prisca* Barrande, 1872.

Distribution. The genus is present throughout Europe in the lower Ordovician (Tremadoc – Llandeilo) and also the Arenig Series of Turkey (Dean 1973). The type species, originally described from the lower Llanvirn of Sarka, Bohemia, has since been recorded from the upper Llanvirn of Bulgaria (Spassow 1958 : 18) and from the Arenig and lower Llanvirn Series of Britain (Whittard 1961 : 177).

Discussion. *Aeglina prisca* Barrande, 1872, designated type species by R. & E. Richter (1954), was considered by Marek (1961) to be conspecific with *Pricyclopyge binodosa* (Murchison, 1859). However, it is here preferred to follow Whittard's later argument (1966 : 287) in favour of considering them as two separate species.

The thoracic and pygidial morphology of *Aspidaeglina* Holub, 1911 is similar to that of *Pricyclopyge* with the exception of the spinose thoracic pleural terminations in *Aspidaeglina*. The cephalon is at present very imperfectly known and further specimens may indicate it to be congeneric with *Pricyclopyge*. *Cyclopyge* Hawle & Corda, 1847 is distinguished from *Pricyclopyge*

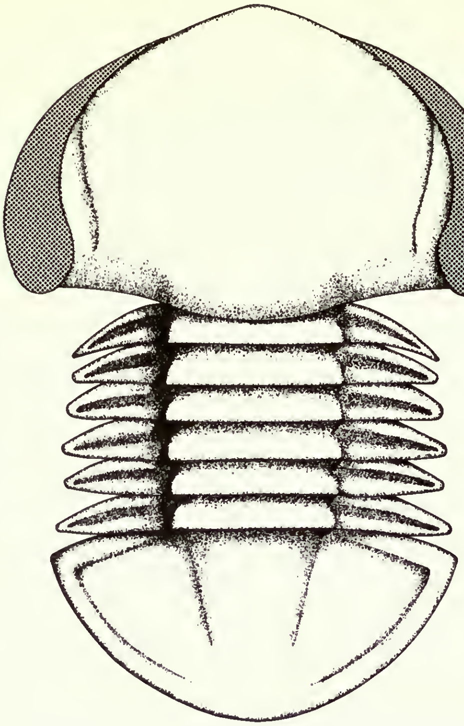


Fig. 2. Reconstruction of *Pricyclopyge wattisoni* sp. nov., *c.* x 3.

by its semicircular pygidium, lack of a large pleural spine on the sixth pleural thoracic segment and by a different configuration of cephalic muscle scars.

Pricyclopyge wattisoni sp. nov.

(Figs 7, 8)

DIAGNOSIS. *Pricyclopyge* with no median glabellar node and somewhat rounded outline to the triangular pygidium; glabellar margins ill-defined posteriorly.

NAME. After the late Mr J. T. Wattison.

TYPE MATERIAL. Holotype, BU 1913 (*ex* Wattison Collection) (Fig. 7), external mould of cranidium and anterior thoracic segment. Paratype, BU 1914 (*ex* Wattison Collection) (Fig. 8), external mould of pygidium.

DIMENSIONS (in mm).	A	J	K		Q_1	R_1	R_2
Holotype	9·5	12·0	10·8		1·6	12·0	6·0
		W	W_1	X	Z		
Paratype		13·0	11·0	4·0	7·4		

For explanation of symbols see Fig. 1.

TYPE LOCALITY AND HORIZON. Both the type specimens are from the *Glyptograptus teretiusculus* Shales in the small quarry at the south-western end of Pen-cerig Lake. This is the only locality from which the species is known.

DESCRIPTION. Cranidium elliptical, consisting almost entirely of large, gently convex, unfurrowed glabella. Cranidium slightly wider than long; posterior margin convex posteriorly. Axial furrow, marked by change of curvature between the flat fixigena and gently convex glabella, gently convex outwards medially; posteriorly indiscernible. Fixigena, present along three-quarters of glabella, very small, forming a narrow palpebral lobe lateral to glabella and expanding slightly into a small triangular area posterolaterally. Facial suture directed anteromedially at posterior margin, becoming parallel to axial furrow. Occipital furrow very shallow, delimiting a narrow (*sag.*) occipital ring. Posterior border furrow very shallow laterally, merging axially with occipital furrow. Librigena and eye unknown.

Pygidium roundedly subtriangular with continuous border which is less pronounced posteriorly. Axis tapers posteriorly; delimited by axial furrow for only about half pygidial length. Articulating half ring and two axial rings visible, anterior one being the more prominent; pleural field smooth.

Discussion. Both the cranidium and the pygidium probably belong to the same species, if not the same individual, because of their close association on the same slab, compatible size, and the fact that they both appear to be best assigned to *Pricyclopyge*.

The species is distinct from all named species of *Pricyclopyge*, although the pygidium described as 'cyclopygid E' by Whittard (1966: 289; pl. 49, figs 14, 15) may belong to this species. However, the Shelve specimen is more rounded in outline and the axis is better defined. The presence of the median doublural spine in the Shelve specimen is of uncertain significance; the doublure is not known in the Builth specimen. *P. binodosa* (Murchison, 1859) differs in that it possesses a prominent median glabellar node and the cephalic and pygidial furrows are better developed. *P. latifrons* (Tjernvik, 1956), from the Ceratopyge Limestone of Sweden, is perhaps most similar to this new species, but the latter differs in having no well-developed median glabellar node nor any transverse terrace lines. *P. obscura* Marek, 1961 differs from *P. wattisoni* in having an elongate (*sag.*) narrow (*tr.*) glabella, while *P. synophthalma* (Klouček, 1916) is distinguished by its much greater median transverse expansion of the glabella and better-defined axial furrow. *P.* (?) *campestris* Koroleva, 1967 is easily distinguished by the well-developed pygidial axis and the clearly-defined cephalic axial furrow. *P. superciliata* Dean, 1973 from the Sobova Formation of Turkey is distinguished by its relatively long glabella, well-incised axial furrow and relatively wide fixigena.

An internal mould of a thorax, It.2837, is provisionally referred to *P. wattisoni* (Fig. 5) as it occurs with the type specimens of this species at Pen-cerig Lake.

Cyclopygid gen. et sp. indet.
(Fig. 13)

Figured specimen. It.2839, internal mould of pygidium. Dimensions (in mm): W, 4·7. X, 1·4. Y (measurement taken to the posterior extremity of the axial furrow), 1·7. Z, 2·8. For explanation of symbols see Fig. 1.

Locality and horizon. Stream section 15 yd (14 m) SW of the old quarry 350 yd (320 m) west of Maesgwynne, in *Glyptograptus teretiusculus* Shales.

Description. Pygidium small, subsemicircular in outline. Axis occupies just under one-third of the width anteriorly and tapers to the rear. Axial furrow well developed anteriorly, but becomes progressively weaker posteriorly, finally dying out altogether at about three-fifths of the distance to posterior margin. Axis merges without interruption into postaxial field; no postaxial furrow present. One well-developed axial ring present. Pleural field gently convex and has one prominent furrowed rib, the furrow becoming more prominent distally. Anterior border narrow (*sag.*) separated by anterior border furrow. Doublure moderately wide, seemingly about half the length of the postaxial field in width, and bears a series of terrace lines parallel to the margin.

Discussion. This isolated pygidium of lower Llandeilo age is very like *Microparia nudus* Whittard, 1961 and *Microparia* (*Degamella*) *gigantea* (Barrande, 1872) in outline, but differs from both in the nature of the furrowing of the axial and pleural regions.

Family **ASAPHIDAE** Burmeister, 1843
Subfamily **ASAPHINAE** Burmeister, 1843
Genus ***NOBILIASAPHUS*** Přibyl & Vaněk, 1965
[= *Pamirotchechites* Balashova, 1966]

DIAGNOSIS (emended from Přibyl & Vaněk 1965 : 277–278). Like *Opsimasaphus* but differs in that glabella is well defined frontally, and laterally with preglabellar field up to two-fifths of cephalic length. Path of anterior branches of facial suture semicircular, intramarginal, subtending an angle of between 90° and 130° frontally. Glabella clearly furrowed with median tongue-like lobe divided by two transverse furrows, posteriorly deflected adaxially. Three small lateral glabellar lobes and two very faint circular muscle areas present lateral to median lobe. Thoracic segments terminate in short blunt spines. Pygidial outline parabolic with up to 17 axial rings. Axial ring furrows and surface sculpture, posteriorly deflected medially, giving central keel to axis, which may be pointed posteriorly. Pleural field with 14 to 16 ribs. Doublure narrow posteriorly, more concave than in *Opsimasaphus*.

TYPE SPECIES. *Asaphus nobilis* Barrande, 1846.

DISTRIBUTION.The genus ranges from the Llanvirn to Ashgill Series. It is present in the Llanvirn – Caradoc (Soudleyan) of Czechoslovakia (Havlíček & Vaněk 1966 : 41, 55; Kříž & Pek 1972 : 165; Přibyl & Vaněk 1965 : 278; Přibyl & Vaněk 1968 : 192); Llanvirn and ? Llandeilo of Spain (Gil Cid 1972, 1972*a*); middle and upper Llandeilo of Wales (herein); Llandeilo of the Pamir, U.S.S.R. (Balashova 1966, 1968); lower Ordovician of France ? (Racheboeuf 1970); Caradoc of Portugal (Thadeau 1947 : 220) and of Sardinia (Laufeld 1973); ? upper Ordovician of Afghanistan (Pillet & Lapparent 1969 : 326).

DISCUSSION. On erecting *Opsimasaphus*, Kielan (1960 : 75–77) discussed '*Asaphus*' *nobilis*, which had been placed previously in *Pseudobasilicus* by some (Reed 1930 : 308; Jaanusson 1953 : 445), and concluded that its generic attribution remained in doubt. Přibyl & Vaněk (1965) erected *Nobiliasaphus*, type species *Asaphus nobilis*, as a subgenus of *Opsimasaphus*. Subsequently, Balashova (1966) erected *Pamirotchechites*, also with *A. nobilis* as type species. Balashova (1968) later assigned *nobilis* to *Pseudobasilicus* and Gil Cid (1972, 1972*a*) followed this. In 1971, however, Balashova accepted *Nobiliasaphus* and gave it full generic status; this was supported by Kříž & Pek (1972).

A full revision of this group of asaphids is beyond the scope of this paper, but the characteristic rearward kink in the pygidial axial ring furrows, so clearly portrayed by Barrande (1852 : pls 31, 32), in particular would seem to necessitate the rejection of close affinity between *Pseudobasilicus* and '*Asaphus*' *nobilis*. Further, this feature, and the better definition of the glabella, long preglabellar field and greater number of pygidial ribs, appear to be consistent differences between *Nobiliasaphus* and *Opsimasaphus*. It is clear, however, that *Nobiliasaphus* is closely related to *Opsimasaphus*, and it seems inappropriate to continue to place *Nobiliasaphus* in the Pseudoasaphidae of Balashova, 1969; both genera are thus included here in the Asaphidae. The relations of these genera to other asaphids are less clear and although they are placed here in the Asaphinae, both show some similarities to the ogygiocaridinid – niobinid group.

The generic placing of specimens described as *O. radiatus* (Salter, 1866*a*) by Whittington (1966 : 71–78) and Ingham (1970 : 18–19) is not entirely certain due to indifferent preservation.

Nobiliasaphus powysensis sp. nov.
(Figs 10, 14–16, 20)

DIAGNOSIS. Glabella occupies about three-fifths cephalic length. Anterior branches of facial suture widely divergent, becoming very nearly marginal; mid-point of eye about one-fifth of cephalic length from posterior margin. Pygidium subparabolic, axis slender, tapering posteriorly with at least 17 axial rings; anterior width about one-eighth of anterior pygidial width. Pleural field with 14–16 ribs. Border region smooth and moderately wide.

NAME. From Powys, Wales.

TYPE MATERIAL. Holotype: It.13553 (*ex* University College, Aberystwyth, UCW 19451/2) (Figs 15, 16), internal and external moulds of entire specimen. Paratypes: It.2924 (Fig. 20), internal and external moulds of disarticulated specimen consisting of cranidium, pygidium and some thoracic segments. I.2857a, internal mould of large pygidium. It.13554, internal mould of pygidium. It.13555 (Fig. 10), internal and external moulds of pygidium. SM A44731 (Fig. 14), external mould of pygidium and part of thorax.

TYPE LOCALITY AND HORIZON. The holotype is almost certainly from the *Nemagraptus gracilis* Shales, in the middle quarry, Llanfawr, Llandrindod (locality recorded in University of Wales, Aberystwyth, catalogue as ' "quarry near Hospital", Llandrindod Wells'). Paratypes It.13554–5 are from the middle quarry, Llanfawr; It.2924 is, and I.2857a and SM A44731 are most probably, from Gwern-yfed-fâch quarry.

DIMENSIONS (in mm).		A	B	C_1	C_2	J	J_1	J_2	K
Paratype	It.2924	*c.* 22·5	13·5	*c.* 3·9	2·2	*c.* 30·0	*c.* 22·0	*c.* 16·5	8·0

		R_1	R_2	Q_1	W	W_1	X	X_1	Y	Z
Holotype	It.13553	*c.* 22·2	5·1	1·2	21·5	16·2	3·0	1·5	10·0	12·7
Paratypes	It.2924	–	–	–	*c.* 42·0	–	5·5	2·3	*c.* 23·0	27·5
	I.2857a	–	–	–	*c.* 108·0	–	16·3	*c.* 7·5	*c.* 69·0	78·0
	It.13554	–	–	–	–	14·2	3·0	1·5	9·9	11·8
	It.13555	–	–	–	26·7	21·8	4·1	1·8	13·2	17·1*
	SM A44731	–	–	–	*c.* 26·4	*c.* 21·4	4·0	1·9	13·9	17·4*

For explanation of symbols see Fig. 1. * – measured on external mould.

DISTRIBUTION. Known only from the two localities yielding the type specimens.

DESCRIPTION. Glabella relatively short, occupying about three-fifths of cephalic length and defined laterally by weak axial furrow, particularly anteriorly; frontally glabella merges into preglabellar

Figs 3–4, 6, 9. *Emmrichops* ? *extensus* sp. nov., p. 113. Figs 3, 6, 9, Lower Llandeilo, left bank of stream section east of Bach-y-graig, 40 yd (37 m) upstream of the point where the footpath enters the wood at the western end of the section, SO 071610. Figs 3, 9, Paratype. Internal mould of cephalon, It.2838. Fig. 3, ×4; Fig. 9, ×7. Fig. 6, Paratype. Latex impression from external mould of pygidium, It.2838, ×3·5. Fig. 4, Lower Llandeilo, ? small quarry at SW end of Pen-cerig Lake (see p. 113); SO 043541. **Holotype.** Internal mould of pygidium showing well-developed doublure, GSM 6142, ×3.

Fig. 5. ? *Pricyclopyge wattisoni* sp. nov., p. 116. Lower Llandeilo, locality as Figs 7–8. Internal mould of thorax, It.2837, ×4.

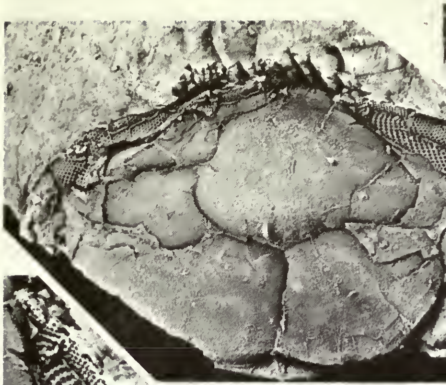
Figs 7–8. *Pricyclopyge wattisoni* sp. nov., p. 115. Lower Llandeilo, small quarry at SW end of Pen-cerig Lake, SO 043541. Fig. 7, **Holotype.** Latex impression from external mould of cranidium, BU 1913 (*ex* Wattison Coll.), ×3. Fig. 8, Paratype. Latex impression from external mould of pygidium, BU 1914 (*ex* Wattison Coll.), ×2·5.

Figs 10, 14–16. *Nobiliasaphus powysensis* sp. nov., p. 117. Fig. 10, Middle-upper Llandeilo, middle quarry, Llanfawr, Llandrindod, SO 066617. Paratype. Internal mould of pygidium, It.13555, ×1·75. Figs 15–16, Middle-upper Llandeilo, ? middle quarry, Llanfawr, Llandrindod (see above), SO 066617. **Holotype.** Internal and external moulds of entire individual, It.13553 (*ex* University College of Wales, Aberystwyth, Collection, UCW 19451, 19452), ×2. Fig. 14, Middle-upper Llandeilo, near Builth Road, Radnorshire (Powys), probably from Gwern-yfed-fâch quarry, ½ ml (805 m) SE of Builth Road station, SO 030526. Paratype. External mould of pygidium showing slight irregularity of rib development, SM A44731, ×2.

Fig. 11. ? *Opsimasaphus* sp. indet. B, p. 121. Lower Llandeilo, small quarry at SW end of Pen-cerig Lake, SO 043541. Mould of dorsal surface of hypostoma, It.2840, ×4.

Fig. 12. Ogygiocaridinid gen. et sp. indet., p. 153. Lower Llandeilo, left bank of stream section east of Bach-y-graig, 40 yd (37 m) upstream of the point where the footpath enters the wood at the western end of the section, SO 071610. Internal mould of meraspid of degree 0, It.2927, ×20.

Fig. 13. Cyclopygid gen. et sp. indet., p. 116. Lower Llandeilo, stream section 15 yd (14 m) SW of the old quarry 350 yd (320 m) west of Maesgwynne, SO 059566. Internal mould of pygidium, It.2839, ×8.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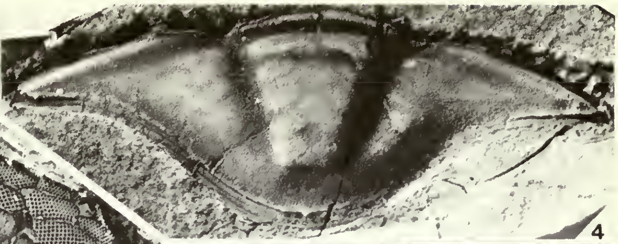
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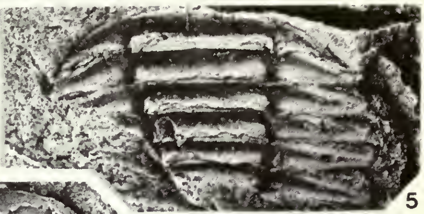
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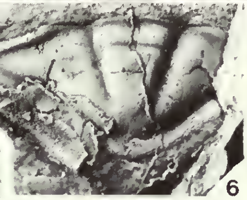
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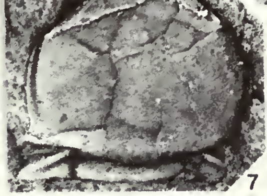
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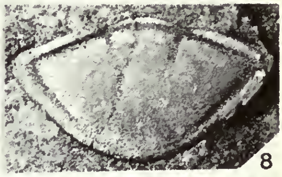
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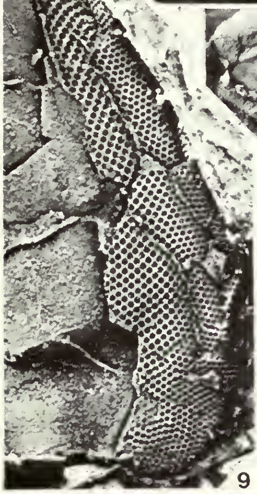
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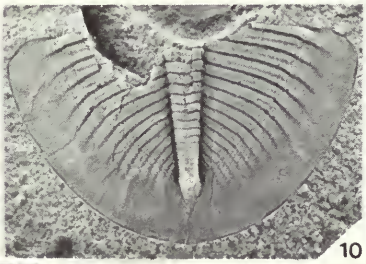
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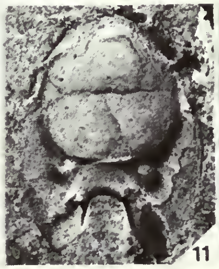
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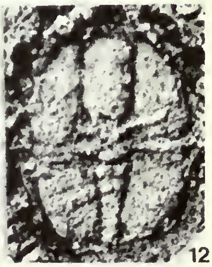
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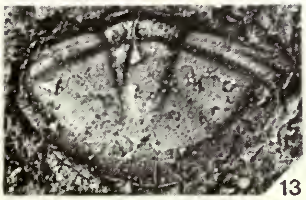
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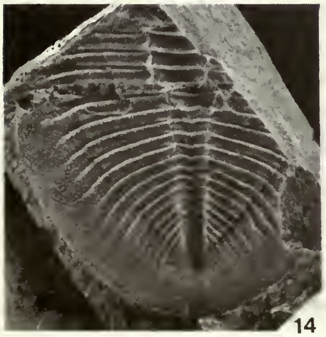
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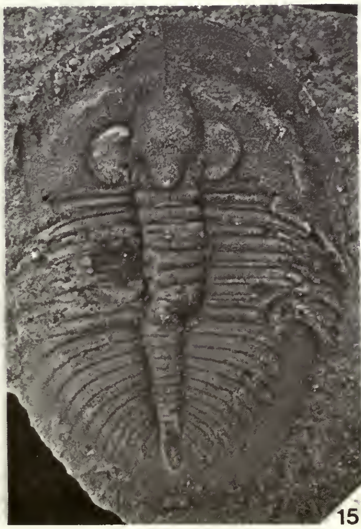
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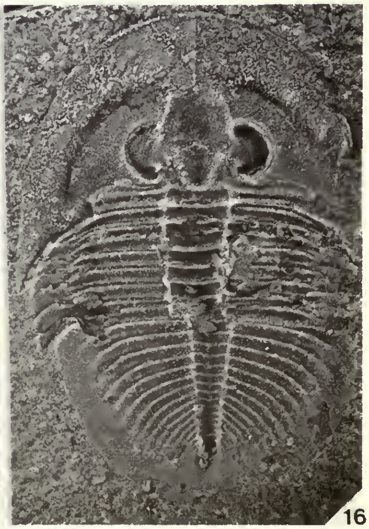
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field with only a very shallow preglabellar furrow. A slight, though distinct, constriction of the glabella developed approximately opposite (*tr.*) posterior of palpebral lobe. Anterior to this, glabella expands slightly, attaining its maximum width just anterior of palpebral lobe; obtusely rounded frontally. Lateral glabellar furrows poorly preserved, but basal pair prominent, declined steeply posteromedially commencing just posterior to mid-point of palpebral lobe, and delimiting a posteriorly-tapering, wedge-shaped median lobe, with small median glabellar node at its posterior extremity. A further very weak pair of furrows may be developed just anterior to palpebral lobe and declined posteromedially at about 45° to sagittal line. Occipital furrow continuous; occipital ring distinct, with posterior margin slightly convex posteriorly. Anterior branches of facial suture widely divergent, subtending an angle of about 90° at the sagittal line, and intramarginal frontally. Frontal area large and nearly flat; low median ridge may extend across the frontal area (Figs 15, 16, 20), but may be an artefact of preservation. Palpebral lobe semicircular and more or less flat. Eye large, crescentic; no traces of lenses known. Immediately to the posterior, facial suture is more or less transversely directed and just in front of the posterior border furrow; laterally it is deflected to cut the posterior margin. Posterior border furrow well developed and straight. Posterior border convex and only slightly narrower (*exsag.*) than occipital ring. Librigena smooth, very gently convex, with wide concave border. Genal spine prominent, extending back to fifth thoracic segment. Cephalic doublure slightly wider than border; median suture present frontally.

Thorax approximately rectangular in outline, though it tapers slightly to the posterior. Axial furrows deep, slightly scalloped and converging slightly towards the posterior. Deep apodemal pit developed in the axial furrow at posterior of each segment. Posterior band on the axial rings, anteriorly convex. Pleural furrow commences at inner anterior corner of pleura and directed slightly obliquely to anterior margin, dying out before it reaches the bluntly-pointed, posteriorly directed pleural termination. Doublure probably underlies about one-third of pleural width.

Pygidium subparabolic with slender axis, occupying from one-sixth to one-eighth of pygidial width anteriorly and tapering uniformly to the rear where it is slightly less than half its anterior width. At least 17 axial rings, possibly as many as 20, are developed, with an apodemal pit, most clearly developed anteriorly, present in the axial furrow at posterior of each ring. Pleural field flat, bearing 14–16 well-defined ribs which bear weak furrows. Distally the ribs are deflected posteriorly, the point of deflection occurring at about two-thirds the way along the anterior ribs, moving progressively to about the mid-point on the shorter, more posteriorly placed ribs. SM A44731 shows slight irregularity in rib development on left pleural field. Border region wide with ribs only just extending onto it. Doublure bears terrace lines oblique to the inner margin; inner edge appears to be scalloped.

Discussion. This new species is clearly distinguished from all known species of *Nobiliasaphus* by the much higher number of pygidial ribs. There are also differences in outline of the pygidium and minor differences in cephalic proportions (see Kříž & Pek 1972, 1974).

Genus ***OPSIMASAPHUS*** Kielan, 1960

Diagnosis. See Kielan 1960 : 75.

Type species. *Opsimasaphus jaanussoni* Kielan, 1960.

Distribution. The genus ranges from the ? lower Llandeilo to Ashgill Series. It is present in the lower Llandeilo of Wales (?) (herein); the Caradoc of Ireland (Brenchley *et al.* 1967, M. Romano personal communication 1973) and northern Poland (Modlinski 1967); the Ashgill of Bohemia, Poland and Sweden (Kielan 1960), Britain (Ingham 1970) and Kazakhstan (Nikitin *et al.* 1968) and possibly of Quebec (Lespérance 1968); ? the lower Ordovician of France (Racheboeuf 1970).

Discussion. With the relatively recent acceptance of *Nobiliasaphus* as a separate genus many of the reported occurrences of *Opsimasaphus* must remain in some doubt until this whole group of asaphids is revised.

? ***Opsimasaphus*** sp. indet. A
(Figs 18–19)

Figured material. It.2925 (Fig. 19), internal mould of incomplete cranidium. Dimensions (in mm): A, 25·5. B, 18·6. J, 39·0. J_1, 28·3. J_2, 22·5. K_2, 14·0. For explanation of symbols see Fig. 1. It.2926 (Fig. 18), fragment of external mould of cranidium.

Locality and horizon. Both figured specimens are from the *Glyptograptus teretiusculus* Shales in the old quarry 570 yd (521 m) north of Wye Cottage.

Description. The single internal mould of an incomplete cranidium shows some similarities to *Nobiliasaphus powysensis*. However, the glabella is relatively longer, occupying nearly three-quarters of the cephalic length, and is relatively wider and much more clearly defined anteriorly. The palpebral lobe bears a distinct furrow. The external mould reveals that at least the frontal part of the glabella bears a sculpture of fine raised ridges lying subparallel to the preglabellar furrow.

Discussion. These two specimens are clearly of the *Opsimasaphus – Nobiliasaphus* type. They are here designated ? *Opsimasaphus* mainly because of the relatively long glabella which is well defined frontally, both of which are features characteristic of *O. jaanussoni*. However, more definite generic assignment must await the discovery of further specimens.

? ***Opsimasaphus*** sp. indet. B.
(Fig. 11)

Figured specimen. It.2840, mould of dorsal surface of hypostoma.

Dimensions. See Fig. 17.

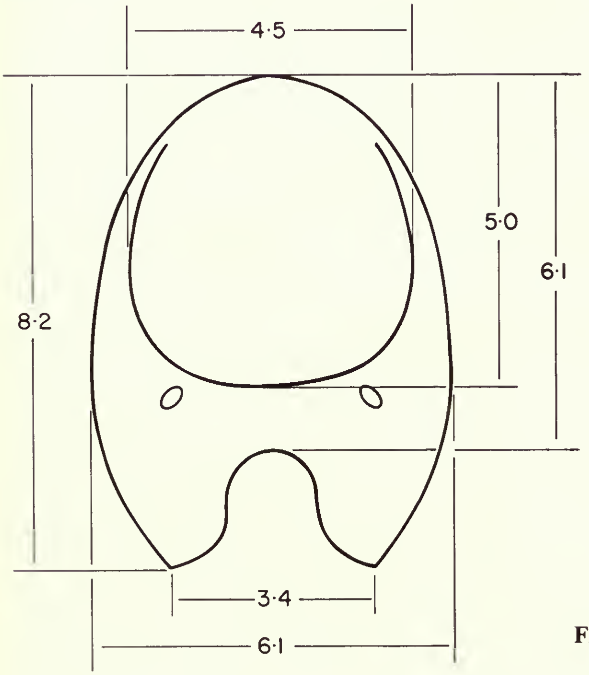

Fig. 17. Diagram showing the dimensions of ? *Opsimasaphus* sp. indet. B.

Locality and horizon. From the uppermost part of the *Glyptograptus teretiusculus* Shales in the quarry at the south-western end of Pen-cerig Lake.

Description. Middle body subcircular, gently convex and not differentiated into anterior and posterior lobes. It is separated from border regions by a clearly-developed border furrow which is deepest posterolaterally. Lateral border widens posteriorly to reach its maximum width just behind the posterior of the middle body. Posterior border is about two-thirds as long (*exsag.*) as middle body, and deeply notched medially. Prominent circular maculae present, situated at base of the projections of the posterior border.

Discussion. This specimen is clearly similar to the hypostoma of *Opsimasaphus*. The placing of isolated hypostomata is, however, difficult and it is possible that it could belong to other asaphid genera having hypostomata with deeply notched posterior borders. *Opsimasaphus* is preferred to *Nobiliasaphus* as an assignment, because other possible ? *Opsimasaphus* specimens are known from beds of similar age within the Builth region. The hypostoma of *Basilicus* Salter, 1849 shows strong similarities, but the present specimen lacks the anterior wings of that genus.

If the placing of either ? *Opsimasaphus* sp. indet. A or B is correct, the occurrence in the lower Llandeilo is of interest as being the earliest record of the genus.

Subfamily **OGYGIOCARIDINAE** Raymond, 1937

Genus ***OGYGINUS*** Raymond, 1912

Diagnosis. The diagnosis of Whittard (1964 : 245–246) is followed here.

Type species. *Asaphus corndensis* Murchison, 1839.

Distribution. The genus is apparently confined to Wales, Salop (Shropshire) and Brittany. Records of the genus from both North and South America (Kayser 1876 : 24; pl. 2, figs 3, 4; Kobayashi 1937 : 495; pl. 5, fig. 9; Rusconi 1950 : 84; Ross 1957 : 494; pl. 42, fig. 7) are very tentative; that of Kayser probably belongs to *Ogygitella australis* Harrington & Leanza (1957 : 142–143) and those of Ross and Kobayashi may be bathyurids and not asaphids. The specimen

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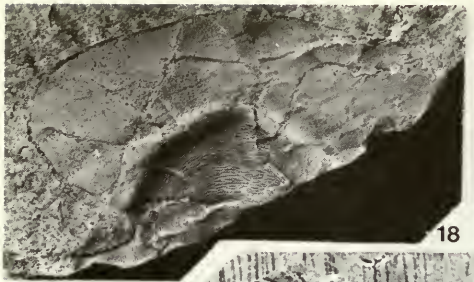
Figs 18–19. ? *Opsimasaphus* sp. indet. A, p. 121. Lower Llandeilo, old quarry 570 yd (521 m) north of Wye Cottage, SO 047538. Fig. 18, external mould of fragment of cranidium showing surface sculpture on glabella, It.2926, ×2. Fig. 19, internal mould of incomplete cranidium, It.2925, ×2.

Fig. 20. *Nobiliasaphus powysensis* sp. nov., p. 117. Middle-upper Llandeilo, quarry at Gwern-yfed-fâch, ½ ml (805 m) SE of Builth Road station, SO 030526. Paratype. Internal mould of cranidium with associated external moulds of thoracic segments and pygidium, It.2924, ×1·5.

Figs 21–33. *Ogyginus corndensis* (Murchison), p. 126. Figs 21, 23, 26, 32–33, Lower Llanvirn, small quarries 600 yd (549 m) east of Upper Gilwern, SO 092582. Fig. 21, internal mould of small meraspid transitory pygidium of unknown degree, It.2849, ×20. Fig. 23, internal mould of transitory pygidium of unknown degree with two pleural ribs and probably two axial rings, It.2875, ×20. Fig. 26, internal mould of entire meraspid of degree 4, showing the single pair of well-developed lateral glabellar furrows and continuous occipital furrow, It.2873, ×10. Fig. 32, internal mould of meraspid of degree 5, showing single pair of lateral glabellar furrows and form of occipital furrow, It.2876, ×10. Fig. 33, internal mould of meraspid probably of degree 6, It.2866, ×10. Figs 22, 31, Lower Llanvirn, eastern end of cliff section on left bank of Camnant Brook, midway between The Court and Pen-dre, SO 088567. Fig. 22, latex impression from external mould of meraspid transitory pygidium of unknown degree, showing trace of one furrow on the left pleural field and a posterior indentation, It.2845, ×20. Fig. 31, internal mould of meraspid of degree 5, with continuous occipital furrow, It.2846, ×10. Figs 24, 28–29, Lower Llandeilo, stream section 15 yd (14 m) SW of the old quarry, 350 yd (320 m) west of Maesgwynne, SO 059566. Fig. 24, latex impression from external mould of meraspid transitory pygidium, showing three pairs of ribs and axial rings and also a prominent posterior indentation, It.2880, ×20. Fig. 28, latex impression from external mould of meraspid transitory pygidium, with two pairs of pleural ribs, It.2863, ×20. Fig. 29, latex impression from external mould of transitory pygidium of unknown degree, It.2864, ×20. Fig. 25, Lower Llandeilo, left bank of stream section east of Bach-y-graig, 65 yd (59 m) upstream of the point where the footpath enters the wood at the western end of the section, SO 072610. External mould of meraspid transitory pygidium of unknown degree, showing two ribs on the left pleural field and three on the right; note also the clear axial furrowing and posterior indentation, It.2881, ×20. Figs 27, 30, Lower Llandeilo, left bank of stream section east of Bach-y-graig, 40 yd (37 m) upstream of the point where the footpath enters the wood at the western end of the section, SO 071610. Internal mould of meraspid of degree 4, showing details of the eye, It.2877. Fig. 27, ×25; Fig. 30, ×10.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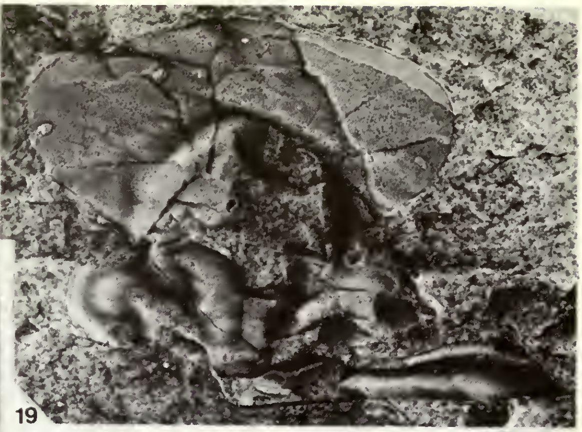
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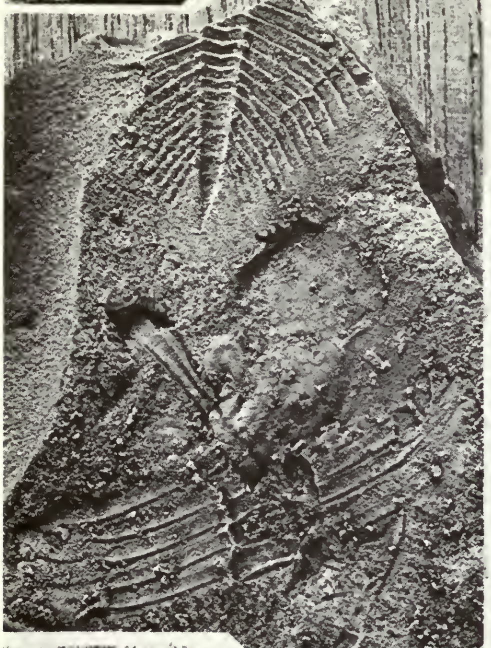
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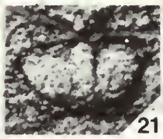
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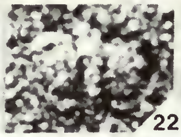
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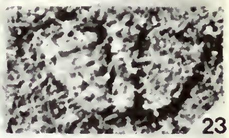
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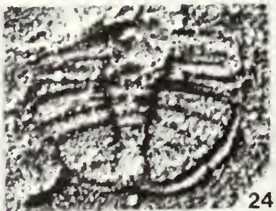
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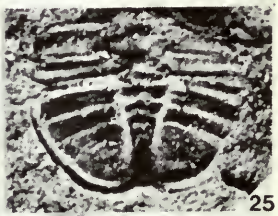
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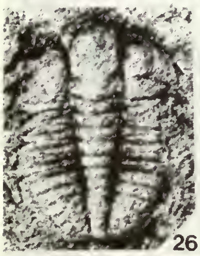
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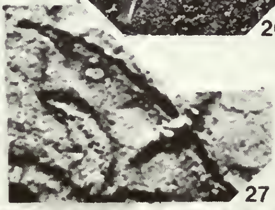
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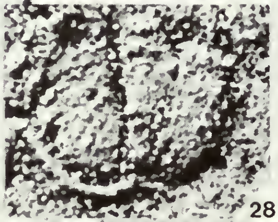
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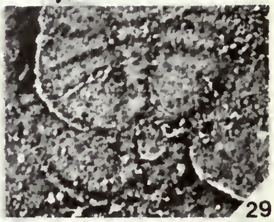
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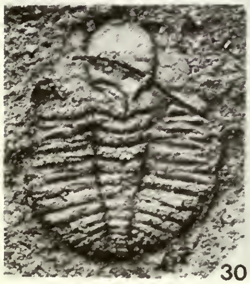
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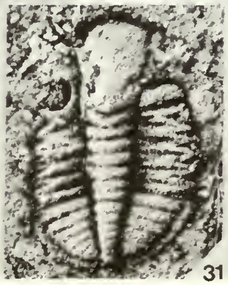
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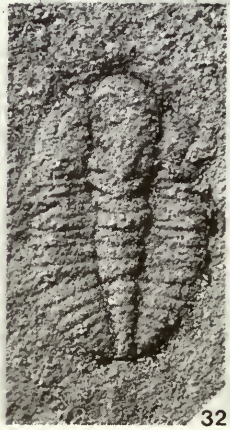
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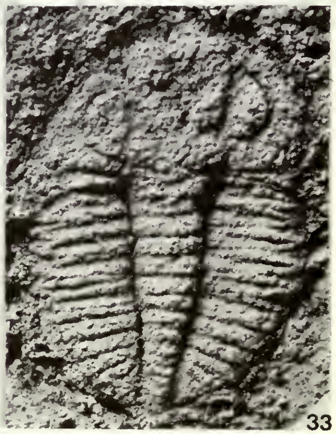
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referred to *Ogyginus* sp. aff. *corndensis* from the lower Ordovician of South Korea (Kobayashi 1934 : 553; pl. 4, fig. 17) has since been placed in *Birmanites* (Kobayashi 1950 : 527). The genus is known to range with certainty from the lower Llanvirn to the upper part of the lower Llandeilo Series, the occurrence in north-west France being of ? Arenig age (Henry 1971 : 66). The genus may also be represented in the Arenig (? *D. hirundo* Zone) of Whitesands Bay, Dyfed (Pembrokeshire) (see Whittard 1964 : 246).

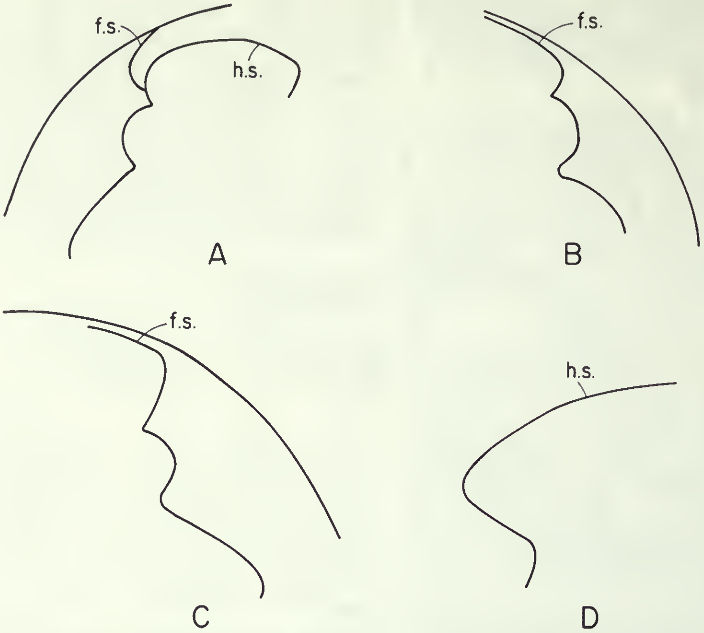

Fig. 34. Diagram showing the position of the anterior branch of the facial suture in *Ogyginus corndensis* (Murchison). A, It.2844 (Fig. 48); B, 59188; C, 59186 (Fig. 52); D, It.2865 (Fig. 58), showing anterior outline of hypostoma. f.s. – anterior branch of facial suture; h.s. – hypostomal suture.

DISCUSSION. Whittard (1964 : 245; pl. 42, fig. 3) believed the facial suture of *Ogyginus* to be marginal and not intramarginal as had been thought previously, though as advocated elsewhere (Hughes 1971*a* : 179) his usage of the terms 'niobiform' and 'isoteliform' to describe the path of the suture anteriorly should be discontinued. However, I suggested (Hughes 1972) that

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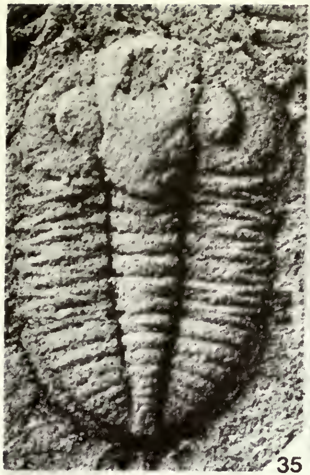
Figs 35–43. *Ogyginus corndensis* (Murchison), p. 126. Figs 35, 37, 39–43, Lower Llanvirn, small quarries 600 yd (549 m) east of Upper Gilwern, SO 092582. Fig. 35, internal mould of meraspid of degree 6, showing slight frontal expansion of glabella and discontinuous occipital furrow, It.2869, ×10. Fig. 37, latex impression from external mould of meraspid of degree 7, showing differentiation of occipital ring into an anterior and posterior region, It.2871, ×10. Fig. 39, internal mould of meraspid of degree 7, with continuous, though medially shallowing, occipital furrow, It.2855, ×10. Fig. 40, internal mould of librigena with eye, It.2870, ×3. Fig. 41, internal mould of smallest known certain holaspis, It.2847, ×5. Fig. 42, internal mould of slightly larger holaspis, It.2854, ×5. Fig. 43, internal mould of still larger holaspis, It.2867, ×5. Fig. 36, Lower Llandeilo, stream section at Wellfield Lodge immediately above where the stream is piped under the road, SO 044528. Internal mould of meraspid of degree 7, with continuous occipital furrow and genal spine extending back to fourth thoracic segment, It.2862, ×10. Fig. 38, Lower Llandeilo, left bank of stream section east of Bach-y-graig, 40 yd (37 m) upstream of the point where the footpath enters the wood at the western end of the section, SO 071610. Internal mould of slightly disarticulated possible holaspis which has retained a continuous occipital furrow; note relatively large eye lenses, It.2878, ×10.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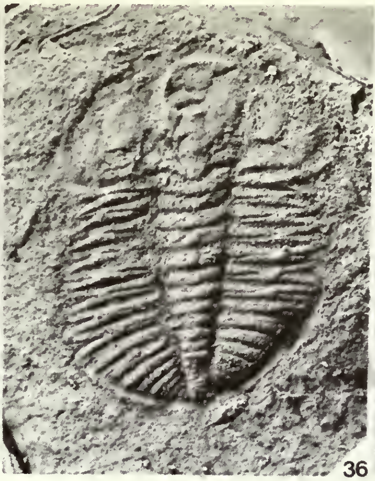
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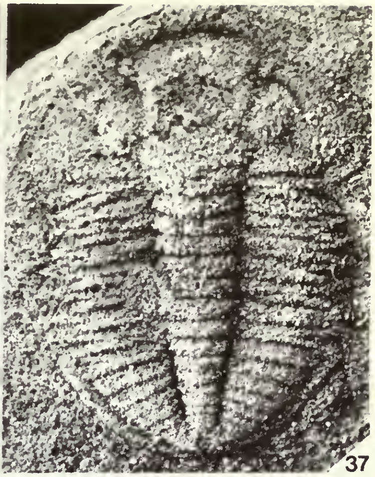
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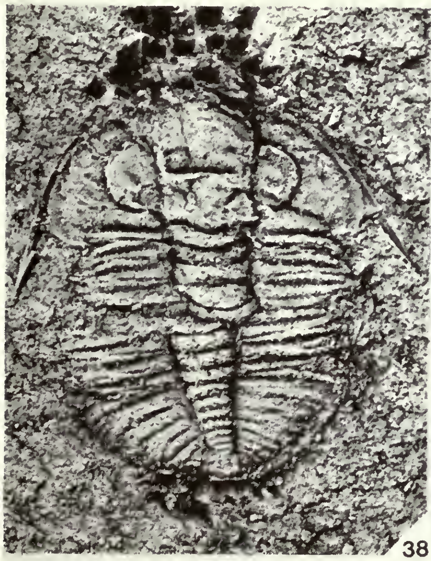
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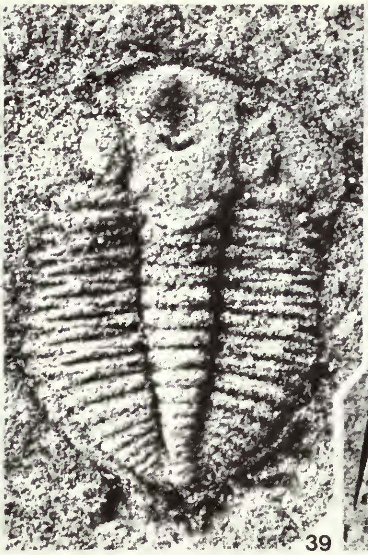
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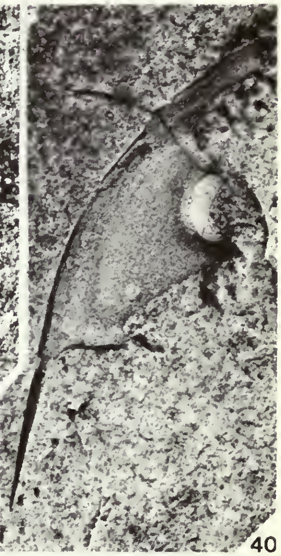
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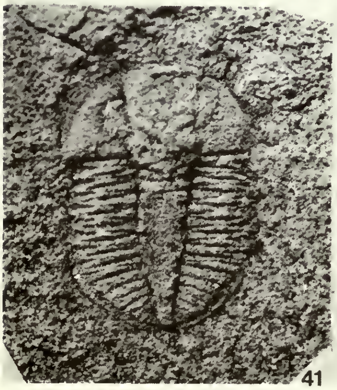
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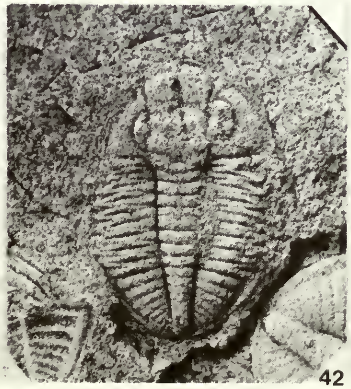
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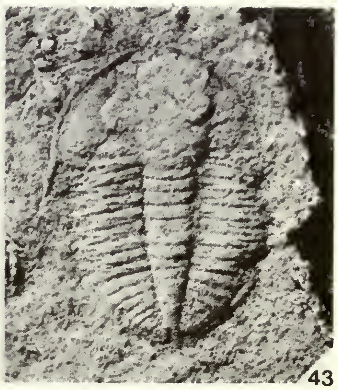
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Whittard was mistaken and that the suture was intramarginal as Salter (1866 : 130) originally described. Proof of this is difficult since the anterior portion of the cephalon is rarely well preserved, presumably because the cuticle was thin. However, It.2844 (Fig. 48) shows the anterior branch of the facial suture on the right side to be intramarginal, at least for the greater part of its course. It is believed that Whittard's interpretation (1964 : 250–251) of specimens 59188 and 59186 (see Figs 34, 52) is incorrect and that the position of the suture in these specimens is as Salter originally described. Against this it must be pointed out that specimens GSM 102135–6 (Whittard 1964 : pl. 42, figs 3, 4) indicate that the suture must be very nearly marginal in some individuals.

Even allowing for the reinterpretation of the course of the facial suture, this genus and *Ogygiocarella* Harrington & Leanza, 1957 are clearly closely related. Differences which support the continued separation of the genera include the general lack of anterior glabellar expansion and the more pronounced furrowing in *Ogygiocarella*, together with the lack of spindle-shaped pleural furrows and the zetoidal axial furrow, and the greater number of pygidial ribs and axial rings.

Hoekaspis Kobayashi, 1937, *Megalaspidella* Kobayashi, 1937 and *Ogygiocaris* Angelin, 1854 resemble *Ogyginus* in many ways, as does *Ogygitella* Harrington & Leanza, 1957, though this latter genus is easily distinguished by its deeply notched hypostoma.

Ogyginus corndensis (Murchison, 1839)
(Figs 21–61, 66)

1839 *Asaphus corndensis* Murchison : 663.
1940 *Ogyginus corndensis* (Murchison) mut. *intermedius* Elles (*pars*) : 406, 428–429, 432; pl. 31, fig. 11 only.
1964 *Ogyginus corndensis* (Murchison); Whittard : 250–254; pl. 42, figs 2–8; pl. 43, fig. 1 (includes full synonymy).
1964 *Ogyginus intermedius* Elles; Whittard (*pars*) : pl. 41, fig. 2 only.
1964 *Ogyginus corndensis* (Murchison) var. *septenarius* Whittard : 254; pl. 43, figs 2–4.
1964 *Ogyginus corndensis* (Murchison) var. *novenarius* Whittard : 254; pl. 43, figs 5–11.
1966 *Ogyginus corndensis* (Murchison); Whittard : 302.
1966 *Ogyginus corndensis* (Murchison) var. *septenarius* Whittard; Whittard : 302.
1972 *Ogyginus corndensis* (Murchison); Hughes : 13–15; fig. 6.

DIAGNOSIS. *Ogyginus* with eye situated at or slightly behind the mid-length. Thoracic axial furrows zetoidal except in meraspis. Pygidium with between seven and nine smooth ribs, approximately ten axial rings.

HOLOTYPE. GSM, Geol. Soc. Coll. GSb 4094 (Fig. 49). Dimensions: T.L. *c.* 66.0 mm; I *c.* 50·0 mm. For explanation of symbols see Fig. 1.

DISTRIBUTION. The species is known from the upper Llanvirn and lower Llandeilo of the Shelve area (see Discussion, p. 135). In the Builth region the species first occurs in the upper part of the lower Llanvirn, and is present until the upper part of the lower Llandeilo. The species is at present unknown outside these two regions.

DESCRIPTION. As this species was fully described by Whittard (1964 : 250–255) a full redescription is unnecessary, except for the hypostoma, of which complete examples are here described for the first time. Comment is made only on features where study of the Builth material adds to, or differs from, Whittard's description.

Complete individuals are ovate, having a length : width ratio of about 3 : 2. Although data are only available for a limited number of complete individuals (see Fig. 44) of a sample from east of Upper Gilwern, these show no evidence of distinct wide and narrow forms. Further, the length–width data for 96 pygidia from the same locality fail to show such forms, although as expected some variation is present (see Fig. 56).

Some cephala are slightly more angular anteriorly than others (Figs 48, 52). Three pairs of short, weak lateral glabellar furrows are developed. The anterior pair, rarely preserved, is situated

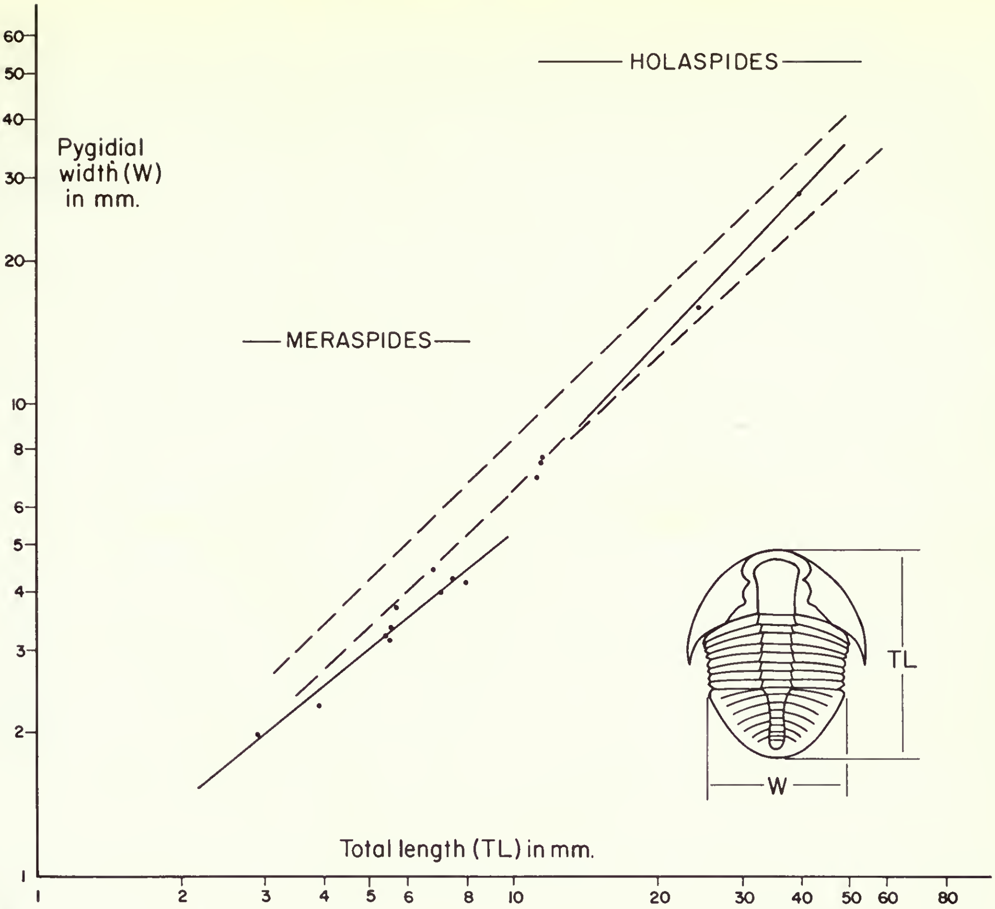

Fig. 44. Graph showing differing regression lines for meraspides and holaspides of *Ogyginus corndensis* (Murchison). The two dashed lines represent total length : width ratios of 6 : 5 and 6 : 4, and illustrate that larger specimens are relatively wider but that distinct 'wide' and 'narrow' forms are not present.

opposite anterior of palpebral lobe and directed slightly anteromedially, and extends about half-way to sagittal line. In common with the other lateral glabellar furrows, abaxial end barely reaches axial furrow (Figs 54, 55). Median pair consists of shorter, transversely-directed furrows situated approximately opposite mid-point of palpebral lobe, extending about half-way to sagittal line and failing to reach axial furrow. Like anterior pair they are rarely preserved. Basal pair most strongly developed and situated opposite posterior of palpebral lobe, being directed posteromedially at between 30° and 40°. They extend slightly further towards sagittal line than do the other two pairs (Figs 54, 55). Lateral occipital lobe virtually isolated by medial convergence of lateral occipital furrow and posterior band furrow (Fig. 55). Immediately anterior to posterior band is a small median glabellar node. On well-preserved internal moulds a low median ridge extends anterior to glabellar node terminating on frontal lobe opposite point where glabella is widest (Figs 55, 61). Posterior border uniform in width and relatively wide, being deflected only very slightly at the fulcrum.

Eye length in young holaspides about one-third of cephalic length; in large specimens eye relatively smaller, the ratio being reduced to about one-fifth. Visual surface approximately crescentic but widens anteriorly (Fig. 40). Eye with up to two thousand hexagonal lenses, situated close to axial furrow, with mid-point between two-fifths and half of cephalic length from posterior margin. Posterior branch of facial suture, immediately posterior to palpebral lobe, makes angle of about 60° with sagittal line. Anterior branch follows a strongly arcuate path from anterior of palpebral lobe, being convex outwards, but is probably entirely dorsal anteriorly (Fig. 48) (see Discussion, p. 124).

Hypostoma, excluding large anterior wings, slightly longer than wide. Arcuate middle furrow separates oval middle body into distinct anterior and posterior lobes. In all but the largest specimen (Fig. 58), anterior lobe oval, long axis directed sagittally, and separated from anterior wing by distinct though shallow anterior border furrow (Fig. 59). In It.2865, total length 15·5 mm, no border furrow is developed and anterior lobe merges anterolaterally with anterior wing. Posterior lobe crescentic and much shorter (*sag.*), occupying only about one-fifth total length. Prominent maculae developed at anterolateral corner of posterior lobe and characterized by their smooth surface. Posterior margin projects backwards sagittally to form median lip; posterior border furrow wide and shallow. Lateral border well developed, but shoulder not prominent. Lateral notch occurs at just over two-fifths the length from anterior. Both dorsal and ventral surfaces of hypostoma, with exception of maculae, bear widely-spaced terrace lines approximately concentric about mid-point of anterior border, but which become progressively more bowed sagittally posteriorly (Fig. 58). The median ridge on posterior half of the anterior lobe in It.2860 (Fig. 60) is not thought to be an original feature as other moulds of the ventral surface fail to show any such ridge.

Anterior margin of hypostoma abuts directly onto cephalic doublure, which widens to form a process flanking anterolateral margin of the anterior wing (Fig. 59). Median suture connects anterior branches of facial suture to hypostomal suture, all being functional. Posterior margin of hypostoma extends for only a short distance behind posterior of eye (Figs 59, 60); fixigena and hypostoma have been displaced slightly to the rear in the holotype (Fig. 49).

Thorax rectangular; about twice as wide as long. Axis occupies about one-quarter of total width and tapers slightly to the rear in small specimens, but becomes nearly parallel-sided in larger individuals (Fig. 46). In very large specimens tapering is again apparent but restricted to posterior half of axis.

Pygidium becomes relatively slightly longer with increase in length. Only anterior five or six axial rings well marked. Articulating half-ring furrows generally well defined, becoming shallower medially. Axis occupies up to nine-tenths of pygidial length in small specimens (Fig. 47), but in large specimens only about three-quarters (Fig. 52). Pleural field gently convex (*tr.*) with eight or nine smooth, unfurrowed, gently convex ribs. Due to *post-mortem* deformation faint furrows may be developed, particularly on anterior ribs. Irregular or asymmetrical development of ribs is very rare, being known on only four specimens (e.g. Figs 50, 51, 53).

Anterior border deflected slightly to posterior laterally with large articulating facets bearing

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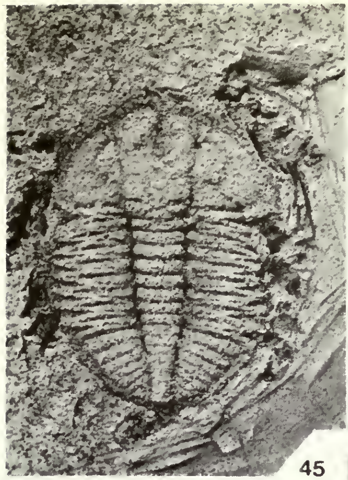
Figs 45–55. *Ogyginus corndensis* (Murchison), p. 126. Figs 45–47, 50–54, Lower Llanvirn, small quarries 600 yd (549 m) east of Upper Gilwern, SO 092582. Fig. 45, internal mould of small holaspis showing general adult form, It.2859, ×5. Fig. 46, internal mould of thorax and pygidium with nine pleural ribs, It.2848, ×1. Fig. 47, internal mould of small pygidium with only seven pleural ribs; note relatively long axis, It.2858, ×6. Fig. 50, external mould of pygidial fragment, showing irregular rib development, It.2857, ×2. Fig. 51, external mould of pygidium, showing incomplete separation of the fifth and sixth pleural ribs on the left pleural field (right side of specimen), It.2872, ×2. Fig. 52, internal mould of nearly complete individual with intramarginal facial suture (see p. 124) and relatively short pygidial axis, 59186, ×$\frac{2}{3}$. Fig. 53, internal mould of pygidium showing incomplete development of furrow separating sixth and seventh pleural ribs, It.2861, ×2. Fig. 54, latex impression from external mould showing glabellar furrows, It.2850, ×2. Fig. 48, Lower Llandeilo, left bank of stream section east of Bach-y-graig, 80 yd (73 m) upstream of the point where the footpath enters the wood at the western end of the section, SO 072610. Specimen with exoskeleton preserved showing intramarginal facial suture, It.2844, ×2. Fig. 49, Weston Beds, near Middleton, Salop (Shropshire). Holotype. Internal mould of damaged specimen; note weak development of eighth pleural rib. GSM Geol. Soc. Coll. GSb.4094, ×1. Fig. 55, Lower Llanvirn, left bank of stream SW of Gilwern, about 100 yd (91 m) from its source, SO 080581. Internal mould of cranidium showing details of occipital ring and node and median glabellar ridge, It.2842, ×4.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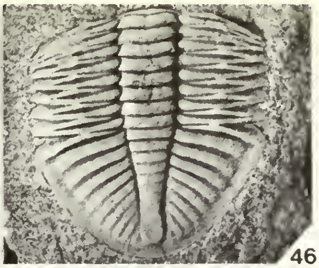
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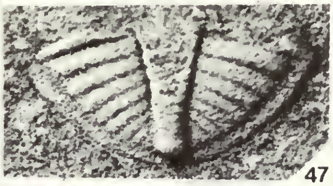
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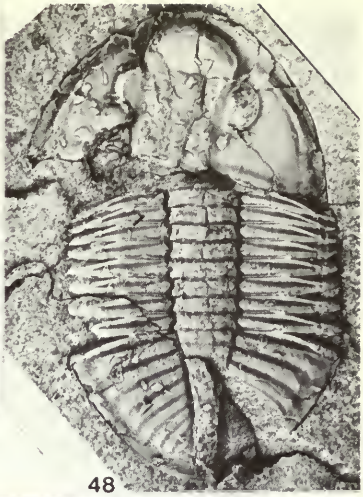
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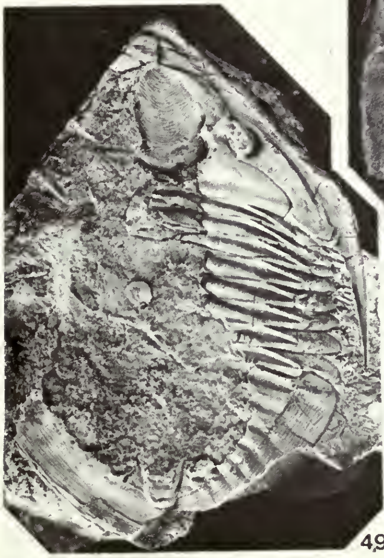
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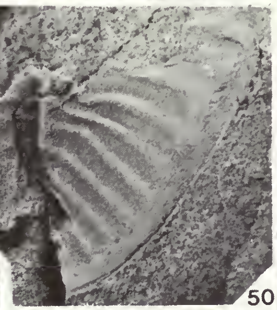
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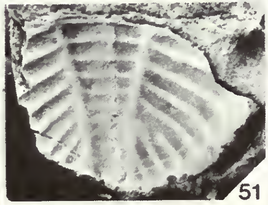
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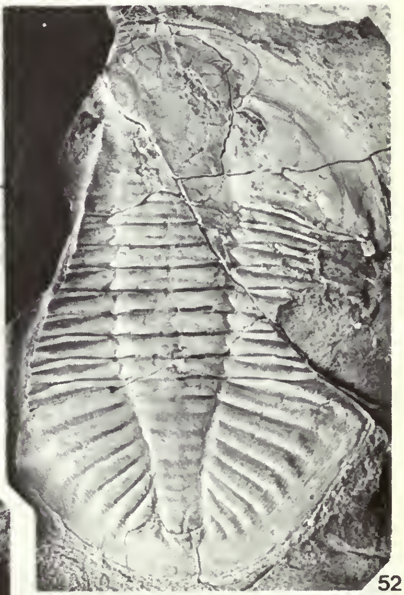
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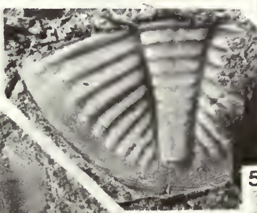
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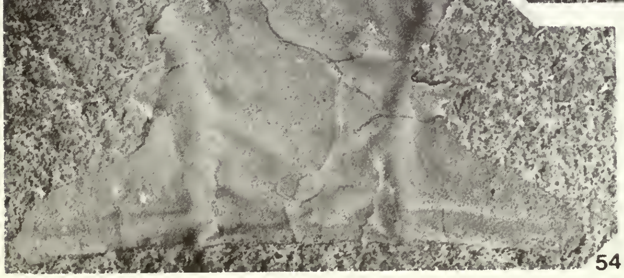
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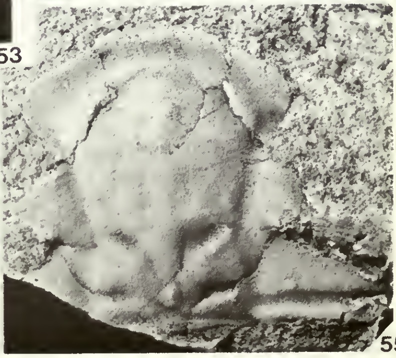
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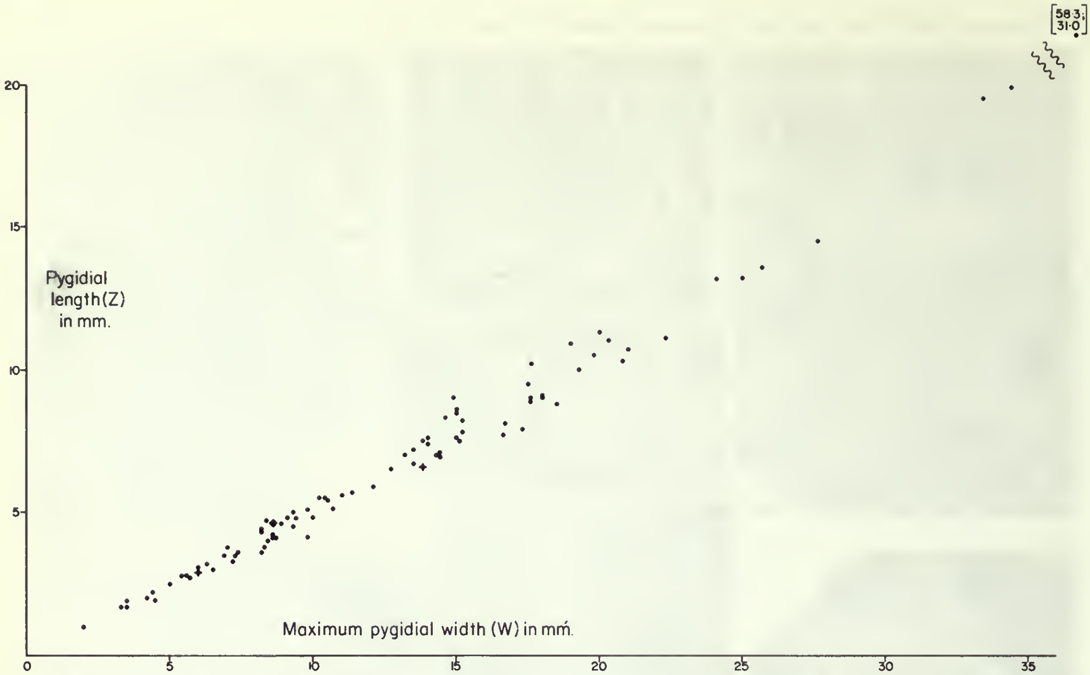


Fig. 56. Plot of length and width of 96 pygidia of *Ogyginus corndensis* (Murchison) from the small quarries 600 yd (549 m) east of Upper Gilwern. + – two specimens.

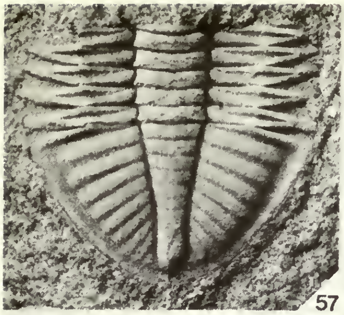
terrace lines; lateral and posterior borders well developed. Doublure relatively wide, being somewhat wider than borders. In small specimens it is generally poorly preserved, but is thought to be relatively narrower than in large specimens where it may be up to one-quarter of pygidial length (Fig. 52). Posteriorly 12–16 relatively widely spaced terrace lines are developed. These lie parallel to the margin on inner half, but are slightly oblique on outer parts. The obliqueness tends to increase towards anterolateral corners and extra lines may be intercalated (Fig. 52). Posteriorly, terrace lines on inner portion of doublure appear to reflect the posterior indentation found in the early meraspid stage.

ONTOGENY. An almost complete suite of meraspid stages is known, principally from the small quarries east of Upper Gilwern.

Figs 57–61, 66. *Ogyginus corndensis* (Murchison), p. 126. Figs 57–61, Lower Llanvirn, small quarries 600 yd (549 m) east of Upper Gilwern, SO 092582. Fig. 57, internal mould of typical pygidium and part of thorax, It.2874, ×3. Fig. 58, mould of dorsal surface of hypostoma, It.2865, ×3·5. Fig. 59, external mould of librigena with mould of dorsal surface of hypostoma and part of cephalic doublure, It.2853, ×3. Fig. 60, mould of ventral surface of hypostoma, with internal mould of librigenae showing median suture, It.2860, ×2. Fig. 61, internal mould of cranidium, showing median pair of lateral glabellar furrows, It.2851, ×4. Fig. 66, Lower Llanvirn, left bank of stream SW of Gilwern, about 100 yd (91 m) from its source, SO 080581. Enrolled specimen, It.2843, ×4.

Figs 62–64. *Ogyginus intermedius* Elles, p. 136. Figs 62, 64, Lower Llanvirn, left bank of upper reaches of Camnant Brook 210 yd (192 m) S 13° W of the fence crossing near the stream source, SO 088575. Fig. 62, internal mould of librigenae with mould of ventral surface of hypostoma, It.2883, ×1. Fig. 64, internal mould of pygidium with ribs furrowed along entire length, It.2882, ×1. Fig. 63, Lower Llanvirn, left bank of upper reaches of Camnant Brook 240 yd (219 m) S 13° W of the fence crossing near the stream source, SO 088575. Internal mould of pygidium with nine ribs furrowed at distal end, It.2885, ×3.

Fig. 65. ? *Ogyginus intermedius* Elles, p. 137. Lower Llanvirn, left bank of Howey Brook, 30 yd (27 m) below the cliff section ½ ml (805 m) ESE of Carregwiber, SO 089582. Internal mould of meraspid transitory pygidium, It.2889, ×10.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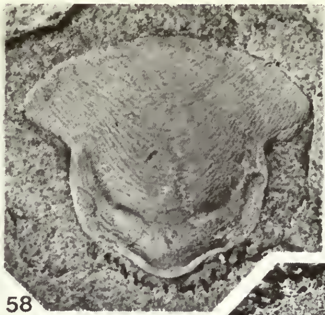
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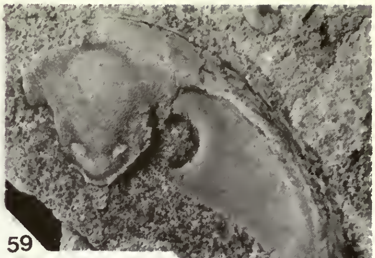
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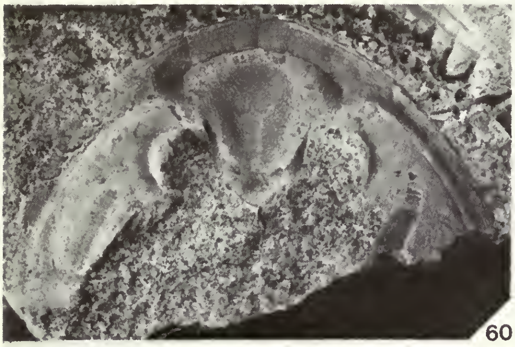
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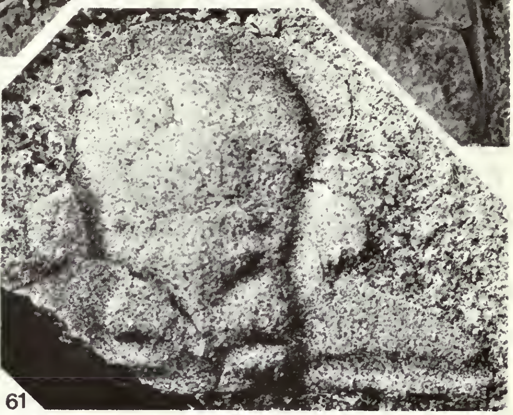
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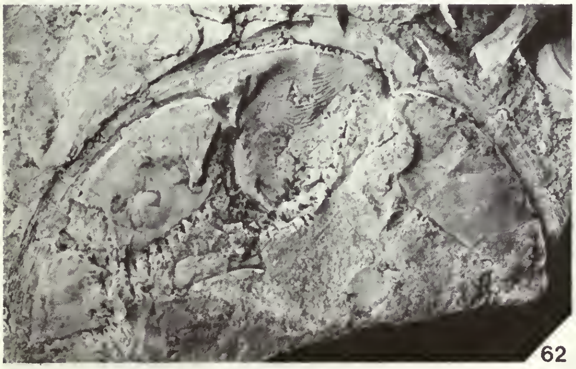
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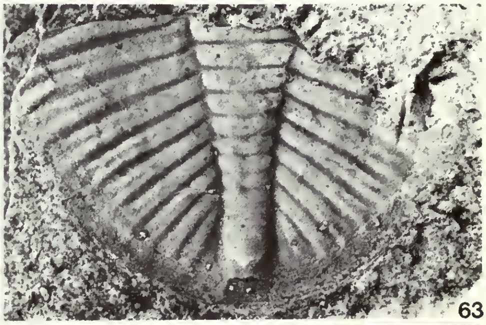
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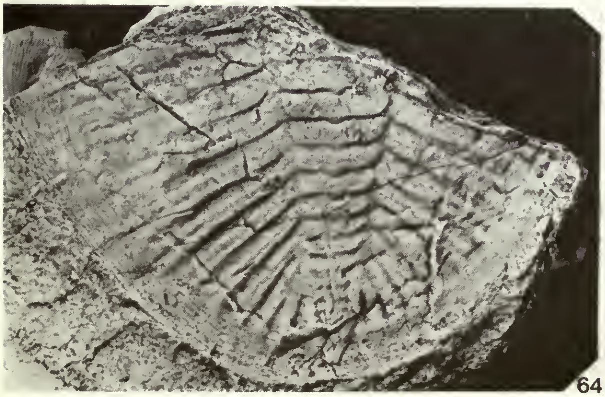
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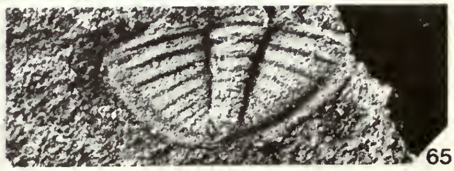
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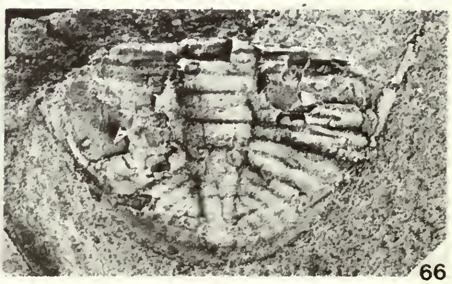
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Degree uncertain. A single isolated globose transitory pygidium, 0·85 mm wide and 0·45 mm long, is roughly semicircular in outline with well-developed posterior indentation (Fig. 22). Axis well defined and tapers posteriorly. Only one pleural rib and at least one axial ring are developed, in contrast to the two ribs developed on transitory pygidium of the degree 0 ogygiocaridinid meraspis described below (p. 153). A further specimen (It.2849) of similar dimensions (Fig. 21) has no ribs or axial rings preserved. The degree to which these specimens belong cannot be determined, though their size suggests that they may be degree 2 or 1, or possibly even degree 0.

Several further isolated transitory pygidia are known which are slightly larger than these two specimens but still smaller than the smallest known transitory pygidium of degree 4 meraspis. These further specimens, whose width ranges from 1·2 to 1·5 mm, are very similar to the smaller ones except that two or three pleural ribs are developed (Figs 23, 24), with up to three axial rings. In all these specimens the ribs occupy, approximately, anterior half of pleural field and become less well developed posteriorly. These transitory pygidia are thought to belong to either degree 2 or 3.

Degree 4. Two complete specimens have lengths of 2·9 mm and 3·2 mm, the cephalon accounting for 1·2 mm and 1·5 mm respectively. Cephalon moderately convex (*tr.*), subsemicircular in outline, being very slightly less than twice as wide as long. Glabella well differentiated, but shows very little, if any, widening of anterior lobe. Single pair of short, clearly incised, lateral glabellar furrows reaches half-way to sagittal line at one-quarter the way along glabella, as measured from the occipital furrow. Occipital ring swollen and bowed backwards sagittally and clearly differentiated by the occipital furrow. Eye well developed, occupies about one-third of cephalic length and has relatively few large lenses (Figs 27, 30). Anterior branch of facial suture not seen, but posterior branch appears to follow a similar course to that of holaspid form. Genal region moderately convex with a pronounced, straight posterior border furrow; posterior border narrow medially, becoming slightly wider distally.

The four thoracic segments, although preservation is not good, appear to be essentially similar to those of holaspides. Axis strongly convex (*tr.*), bounded laterally by well-developed axial furrows. Pleural region appears to possess the typical spindle-shaped pleural furrows, with the fulcrum occurring at about three-quarters of the length out from the axial furrow.

Transitory pygidia approximately semicircular, 2 mm wide and strongly convex (*tr.*) with well-defined convex axial region. Anterior portion of the axis tapers gently to the rear, whilst posterior portion is parallel-sided. Up to nine axial rings developed with at least four ribs on strongly convex pleural field. Outer region of pleural field steeply declined, reaching maximum posteriorly where it is nearly vertical. Border relatively wide laterally and flat, being about one-tenth of pygidial length in width, becoming narrower posteriorly where a shallow terminal incurvation is developed medially.

Degree 5. Two complete specimens, It.2846 and It.2876 (Figs 31, 32), are 3·3 and 3·9 mm long with cephala 1·5 and 1·7 mm respectively. Cephalon roughly semicircular, only a little over one and a half times as wide as long. Glabella moderately convex (*tr.*) with no frontal expansion. The single pair of lateral glabellar furrows differs from that of degree 4 in being directed posteromedially rather than transversely. Occipital ring swollen, clearly differentiated by deep occipital furrow which is transversely directed for a short distance laterally before bending to lie parallel to posterior margin of occipital ring (Fig. 32). This curved central portion of the furrow is considerably shallower than lateral parts, thus anticipating the condition found in degree 6 which lacks central portion of the furrow. Eye well developed, occupies about one-third of cephalic length. Anterior branch of facial suture not known; course of posterior branch similar to that of adult.

The five thoracic segments are typically those of *Ogyginus*, except that axial furrow is more or less straight and shows little sign of the zetoidal shape it so characteristically assumes in the adult form.

Transitory pygidia semicircular, 1·0 mm and 1·2 mm long and 2·1 mm and 2·3 mm wide respectively. Axis shows typical adult outline and has up to seven axial rings. Pleural field moderately convex with six or possibly seven ribs. Border region flat with maximum width equal to one-ninth of pygidial length, becoming narrower and less well defined posteriorly. Preservation is such that it is impossible to determine any posterior indentation.

Degree 6. Only two specimens (It.2869, Fig. 35 and SM A51177) certainly of degree 6 are known; they are about 5·4 mm and 4·2 mm in length, with cephala 2·2 mm and 1·7 mm long respectively. One further specimen (It.2866, Fig. 33) may be of degree 6, but transitory pygidium has overridden the thorax slightly so that no definite count can be made of thoracic segments. Length of this specimen is also about 5·4 mm. Cephalon roughly semicircular in outline, though only just over one and a half times as wide as long. Although the anterior is poorly preserved, the well-defined glabella clearly expands frontally. Single pair of lateral glabellar furrows directed posteromedially as in degree 5. As in earlier degrees, occipital ring swollen and bowed backwards sagittally but occipital furrow no longer continuous, being represented by two short, transversely-directed laterally-placed furrows. Eye well developed and occupies about one-third of cephalic length. Course of anterior branch of facial suture not discernible; that of posterior branch as in adult. Posterior border furrow clearly developed and straight; posterior border narrow medially, widening laterally.

Thoracic segments have the same general form as the adult. Fulcrum, however, situated three-fifths way along pleura as measured from axial furrow, and axial furrow has not attained typical zetoidal shape.

Transitory pygidium only very slightly less than twice as wide as long. Axis clearly differentiated and same shape as in adults, with at least seven and possibly ten axial rings. Pleural region convex, being steeply declined posteriorly. Seven or eight ribs appear to be present. Border region varies in width between one-eighth and one-ninth of pygidial length and is nearly horizontal laterally, becoming narrower and less well defined posteriorly.

Degree 7. Three complete specimens known (It.2855, Fig. 39; It.2871, Fig. 37; It.2862, Fig. 36). Preservation of It.2855 is superior to that of the other two and the following is based mainly on this specimen. Total length 5·5 mm (5·7 mm in It.2871; 4·7 mm in It.2862) with cephalon 2·2 mm in both It.2855 and It.2871 (1·9 mm in It.2862). Cephalon semicircular with glabella expanding frontally (see It.2871). Single pair of lateral glabellar furrows directed transversely. Eye occupies approximately one-third of cephalic length. Occipital furrow in It.2855 entire and shows very little, if any, shallowing medially. It.2871, however, exhibits differentiation of occipital ring into anterolateral lobes and a posterior band as is found in the adult form. In It.2862 occipital furrow still appears continuous medially as in It.2855. Course of both anterior and posterior branches of facial suture appears to be similar to that in holaspides. In It.2862 a short genal spine is present, reaching back as far as fourth thoracic segment. Hypostoma, although not well preserved, appears to be similar to that of adult (It.2855, Fig. 39).

Thorax is essentially like that of adult form except that axial furrow has not attained the typical zetoidal shape.

Transitory pygidium showing seven, possibly eight, pleural ribs in It.2855, but only five or six in It.2871. Axial furrowing not well preserved, but there appear to be at least six axial rings. Border region horizontal laterally, in marked contrast to the steep outer portion of the pleural region, and about one-eighth of pygidial length in breadth. Posteriorly border region becomes narrower and less well defined.

Young holaspides. The smallest specimen, total length 6·8 mm, is not well preserved (Fig. 41), but its length is about 1·2 times greater than that known for any meraspis. Occipital ring still somewhat swollen although posterior band clearly present. A possible young holaspis (It.2878, Fig. 38) still retains a deep, continuous furrow. Eye slightly larger relative to the length of the cephalon than in meraspides, and set well to the posterior. Eye lenses are few and relatively large (Fig. 38). Short genal spine present.

Thorax closely resembles that of larger individuals, except that axial furrow does not show the typical zetoidal shape.

Pygidium relatively wide, just over two and a half times as wide as long. Posteriorly axial rings and pleural ribs poorly preserved, but only seven ribs appear to be developed. Pygidium less strongly convex and with less narrowing of the border region posteriorly than in meraspides. No posterior indentation developed.

A slightly larger specimen (It.2854, Fig. 42), length 7·1 mm, shows eight ribs present on the pleural field.

Discussion of development. Table 1 shows that specimen size, as measured by its total length, is not by itself indicative of a particular meraspid degree; this may in part at least be a reflection of varying amounts of tectonic deformation. If, however, specimens from the single locality east of Upper Gilwern are considered alone, then there is a progressive increase in total length, although at times very small, with increase in meraspid degree. There is no constant growth factor between each degree (see Table 2); this may be due to the paucity of data or to there being more than one instar in some or all degrees.

Table 1. Measurements and rib counts on meraspid and young holaspid specimens of *Ogyginus corndensis* (Murchison). For explanation of symbols see Fig. 1. * – specimen from the small quarries 600 yd (549 m) east of Upper Gilwern. All measurements in mm.

Specimen Number	T.L.	A	C	C_1	C_2	W	Z	Pleural ribs		Axial rings	Degree
								Left	Right		
It.2845	–	–	–	–	–	0·85	0·45	1	?	1+ ?	?
It.2849*	–	–	–	–	–	0·85	0·50	?	?	?	?
It.2875*	–	–	–	–	–	1·2	0·70	2	2	2+ ?	?
It.2880	–	–	–	–	–	1·3	0·85	3	3	3+ ?	?
It.2863	–	–	–	–	–	*c.* 1·5	*c.* 0·95	2	2	3+ ?	?
It.2881	–	–	–	–	–	*c.* 1·5	0·80	2	3	3	?
It.2873*	2·9	1·2	–	–	–	2·0	1·0	4+ ?	4+ ?	6, ? 7	4
It.2877	3·2	1·5	–	0·55	–	2·3	1·0	4+ ?	5+ ?	9	4
It.2846	3·3	1·5	–	–	–	2·1	1·0	4+	6, ? 7	7+ ?	5
It.2876*	3·9	1·7	0·8	0·6	0·3	2·3	1·2	5, ? 6	5, ? 6	5, ? 6	5
SM A51177	4·2	*c.* 1·7	0·6	0·7	–	3·1	1·3	7	7	? 9	6
It.2866*	*c.* 5·4	*c.* 2·3	–	0·8	–	3·2	1·4	?	6+	8	? 6
It.2869*	*c.* 5·4	*c.* 2·2	0·95	0·75	0·5	3·2	1·7	7	8	7, ? 10	6
It.2862	4·7	1·9	–	–	–	3·1	1·4	7, ? 8	7, ? 8	4+	7
It.2855*	5·5	2·2	1·05	0·75	0·4	3·4	1·6	7, ? 8	7, ? 8	6+ ?	7
It.2871*	5·7	2·2	–	–	–	3·7	1·7	5, ? 6	5, ? 6	?	7
It.2878	*c.* 5·1	*c.* 2·0	–	0·8	–	3·3	1·4	?	? 8	8+	? holaspis
It.2847*	6·8	*c.* 2·9	*c.* 1·4	*c.* 1·0	*c.* 0·5	4·5	1·9	? 7	? 7	?	holaspis
It.2854*	7·1	2·8	–	–	–	4·0	1·8	8	8	6+	holaspis

Table 2. Mean lengths (T.L.) and growth factors between meraspid degrees of *Ogyginus corndensis* (Murchison) from the small quarries 600 yd (549 m) east of Upper Gilwern. 8* taken as the smallest two holaspides known which are assumed to belong to the same instar. All measurements in mm. n – number of specimens.

Degree	Mean T.L.	n	Growth factor
4	2·9	1	1·33
5	3·9	1	*c.* 1·38
6	*c.* 5·4	2	*c.* 1·04
7	5·6	2	1·24
8*	6·95	2	

The most interesting morphological feature in the ontogeny of the species is that of the development of the occipital ring and associated features. In general their development shows a progressive change towards the condition found in the adult form, with the deep continuous occipital furrow of degree 4 being reduced to short, transversely-directed furrows by degree 6, with the posterior band appearing in degree 7. However, there are some apparent exceptions, e.g.

It.2855 of degree 7 (Fig. 39) clearly shows a deep continuous occipital furrow with little shallowing medially; a similar condition is found in a ? young holaspis (Fig. 38). The earliest stage in which the differentiation of the occipital ring into anterolateral lobes and a posterior band occurs is degree 7. A latex impression from an external mould (Fig. 37) clearly shows this, although an internal mould of the same degree shows no such differentiation. In earlier degrees there are no such differences apparent between internal and external moulds.

Whilst it is considered that specimens It.2845–6 from the lower Llanvirn belong to *O. corndensis*, the possibility remains that they may represent meraspides of *Ogyginus intermedius* Elles (see p. 136) which may be present at the same locality. The specimens are here assigned to *O. corndensis* on account of their similarity to other mersapides of this species, a holaspis of which is known from the locality. The lack of a distal furrow on the anterior rib may not preclude it from *O. intermedius*, as the ontogeny of the latter species is virtually unknown at present. It may be that early, if not all, meraspides of these two species are indistinguishable.

BIOMETRICAL DATA. Abundant well-preserved material has yielded considerable data which are summarized in Tables 3 & 4.

Table 3. Bivariate statistics for holaspid specimens of *Ogyginus corndensis* (Murchison) from the small quarries 600 yd (549 m) east of Upper Gilwern. All measurements in mm. For explanation of symbols see Fig. 1.

x: y	$\bar{x}$	var. x	$\bar{y}$	var. y	r	r_e	α	var. α	a	var. a	n
A : C_1	12·99	21·15	2·66	0·28	0·93	0·93	0·57	0·0085	–	–	7
A : C_3	12·99	21·15	5·60	4·10	1·00	1·00	1·02	0·0013	0·44	0·0002	7
B : J	19·80	159·78	11·80	56·78	1·00	1·00	1·00	0·0006	0·60	0·0002	12
B : J_1	10·28	42·52	9·91	53·41	1·00	1·00	1·13	0·0005	–	–	18
B : K_2	9·86	35·40	7·09	21·99	1·00	1·00	1·08	0·0003	–	–	30
J : J_1	20·79	177·87	12·01	84·81	0·99	1·00	1·16	0·0009	–	–	9
K_2 : K_1	7·03	21·37	5·84	14·90	1·00	1·00	1·01	0·0003	0·84	0·0002	28
R_1 : Q	16·50	73·73	8·04	15·47	1·00	1·00	0·95	0·0007	0·46	0·0002	8
R_1 : R_2	16·50	73·73	4·29	4·14	1·00	1·00	0·92	0·0006	–	–	8
R_1 : R_4	17·14	82·16	17·63	85·42	1·00	1·00	0·99	0·0008	1·02	0·0008	7
R_2 : R_3	4·35	4·77	4·10	5·05	1·00	1·00	1·08	0·0005	–	–	17
R_4 : R_3	19·70	206·39	4·83	14·58	1·00	1·00	1·07	0·0002	–	–	13
W : Z	13·66	61·90	7·09	19·03	0·99	1·00	1·06	0·0001	–	–	88
W : X	13·60	62·53	3·03	3·18	0·99	0·99	1·01	0·0001	0·23	0·00001	94
W_1 : Y	11·09	39·61	6·07	13·32	0·99	0·99	1·05	0·0001	–	–	107
Z : Y	7·48	23·85	6·63	17·49	1·00	1·00	0·97	0·00002	–	–	123
Y : X	6·38	14·11	3·07	3·16	0·99	0·99	0·98	0·0001	0·47	0·00003	131

Table 4. Measurements of hypostomata of *Ogyginus corndensis* (Murchison) from the small quarries 660 yd (549 m) east of Upper Gilwern. First three specimens are moulds of the dorsal surface, the last two, moulds of the ventral surface. All measurements in mm. For explanation of symbols see Fig. 1.

	H_1	H_2	H_3	H_4	H_5	H_6
NMW 68.376.G208	5·3	4·6	3·7	2·4	–	4·2
It.2853	9·0	8·1	6·5	4·0	*c.* 10·2	6·0
It.2865	15·5	13·0	11·3	7·0	18·5	13·0
It.2860	10·2	8·9	7·0	5·0	10·7	6·0
NMW 68.376.G209	10·6	9·5	7·5	4·5	–	–

DISCUSSION. Although the holotype is from the Weston Beds, near Middleton, Salop (Shropshire), Salter (1866) based his description and figures mainly on specimens from Builth where the species is very abundant.

Although the forms occurring in the Builth and Shelve regions clearly belong to a single species, there is an interesting difference in the stratigraphical distribution of the various forms based on the number of pygidial ribs present. Whittard (1964 : 254) proposed the two varieties *O. corndensis* var. *septenarius* and *O. corndensis* var. *novenarius* to accommodate forms with seven and nine ribs. In the Builth region, unlike Salop (Shropshire), all three forms are found together in the Llanvirn, although the vast majority of specimens have eight ribs. In the lower Llandeilo, however, eight- and nine-rib forms occur in about equal numbers, with seven-rib forms occurring only rarely. In the Shelve region, however, eight-rib forms are restricted to the Llanvirn. Seven-rib forms, which as in the Builth region are rare, occur with eight-rib forms in the Llanvirn excluding the topmost beds (Betton Beds). The nine-rib form occurs with eight-rib forms in the Betton Beds, but is the only form occurring in the Llandeilo. Although the proportion of the various forms within an assemblage has a similar stratigraphical significance in both regions, it is felt that there is little justification for formal recognition of three subspecies. It seems likely the species was evolving under a selection pressure favouring an increased number of ribs, which differed in the two areas.

Whittard (1964 : 253) indicated the distinctions between *O. corndensis* and *O. grandis* Whittard, 1964, *O. porcatus* Whittard, 1964 and *O. intermedius* Elles, 1940. To these may be added *O. armoricanus* (Tromelin & Lebesconte, 1876), redescribed by Henry (1971 : 66–68), which is distinguished by its short genal spine, lack of well-developed occipital ring and lack of occipital node.

Two possible examples of enrolled specimens are known but both are flattened and may be the result of the disarticulated parts of an exuvia being preserved on top of one another.

Ogyginus intermedius Elles, 1940

(Figs 62–64, 68, 71–73, 75)

1940 *Ogyginus corndensis* (Murchison) mut. *intermedius* Elles (*pars*) : 395, 397–398, 428–429; pl. 31, fig. 10, *non* fig. 11.

1964 *Ogyginus intermedius* Elles; Whittard (*pars*) : 246–248; pl. 41, figs 1, 3, 4, *non* fig. 2.

1966 *Ogyginus intermedius* Elles; Whittard : 302, 305.

DIAGNOSIS. *Ogyginus* with relatively small eye situated well to the anterior; glabella expanding onto anterior border. Nine or ten ribs on pleural field with short pleural furrow on distal portion of anterior ribs.

HOLOTYPE. SM A10087 (Fig. 73), internal mould of complete specimen. Dimensions (in mm): T.L., 61·7. A, 20·3. C, *c.* 11·2. C_1, *c.* 3·0. C_2, 6·7. C_3, *c.* 8·2. I_1, *c.* 41·1. K_2, 13·5. Q, 18·9. Q_1, 2·5. R_1, 38·2. R_3, 8·0. R_4, 38·4. W, 38·0. X, 7·8. Y, 18·7. Z, 22·5. For explanation of symbols see Fig. 1.

TYPE LOCALITY AND HORIZON. *Didymograptus bifidus* Shales south-east of Elusendy, Golden Grove, near Llandeilo.

DISTRIBUTION. Elles (1940 : 429) originally recorded the species from the lower Llanvirn of the Llandeilo and Builth regions together with rare occurrences in the upper Llanvirn and Llandeilo of Builth. Whittard (1964 : 248) found the species to be restricted to the lower Llanvirn in the Shelve region, and noted that it was also present in the *bifidus* fauna from west of Llan Mill, Dyfed (Pembrokeshire). Specimens identified as *O. intermedius* from the upper Llanvirn and lower Llandeilo of the Builth region by Elles are here placed in *O. corndensis*, so that the species is now restricted to the lower Llanvirn throughout the Anglo-Welsh region.

In the Builth district the species is most common in the beds exposed in the upper reaches of the Camnant Brook, where it is more abundant than *O. corndensis*. The only other localities within the area where it is certainly present are the 'cliff' section, Howey Brook, Hendy Bank and Frank's Bridge. Elles (1940 : 398) also records it from east of Bwlchyfedwen, but no specimens have been traced to confirm this.

DESCRIPTION. Comment is made only on features in which the Builth material differs from, or adds to, Whittard's redescription (1964 : 246–248). Cephalon known in the Builth region from very few rather poor fragmentary specimens. Three pairs of lateral glabellar furrows appear to be present together with a discontinuous occipital furrow (Fig. 68), although it is uncertain which depressions are true lateral glabellar furrows and which are due to compression. Anterior and median pairs situated approximately opposite small palpebral lobe, with anterior pair directed slightly anteromedially and median pair more or less transverse. Posterior pair situated about half-way between median pair and occipital furrow and directed posteromedially. Lateral glabellar furrows extend no more than about three-quarters of the way to sagittal line (Fig. 68).

Thorax known only from a few poorly-preserved specimens. However, some larger specimens have an axial furrow of moderately well-developed zetoidal form, whilst others show the supposedly more characteristic scalloping (Fig. 68).

Pygidium with axis tapering over its anterior half and well defined by deep axial furrow. Eleven or twelve axial rings may be developed, together with a short terminal piece. Ring furrows continuous though considerably shallower medially. Nine or ten ribs may be developed (Figs 63, 71), with short, shallow furrows present on the distal portions of up to the first six ribs (Fig. 63). The furrows along the entire length of the ribs in It.2882 (Fig. 64) are thought to be the result of compression. It.2886 shows a rib which apparently bifurcates on the right pleural field (Fig. 75). Doublure relatively narrow, in width only about one-eighth of pygidial length and bearing terrace lines.

A single slightly distorted isolate pygidium is known which may represent an immature example of this species (Fig. 65). It shows at least eight axial rings. Although they are poorly defined posteriorly it appears that only eight ribs are present, the anterior one having a short furrow present distally.

The presence of the furrow on the anterior rib suggests that this may belong to *O. intermedius* rather than *O. corndensis*. The development of only eight ribs suggests that the specimen may be of a late stage meraspis rather than a young holaspis. In size it is clearly comparable to meraspides of *O. corndensis* of degree 7.

Discussion. About 30 specimens are known from Builth and they show more variation in the number of pygidial axial rings and pleural ribs than those (not more than 15) known from the Shelve area (Whittard 1964 : 246–248; 1966 : 302). In the light of the variation in the number of pygidial ribs in *O. corndensis* it is not surprising to find a similar variation in *O. intermedius*. The moderately well-developed zetoidal aspect of the axial furrow on the thorax of some large specimens may reflect inherent variation, as in *O. corndensis*.

Whittard (1964 : 246, 248) considered *Ogygiocaris henningsmoeni* conspecific with *O. intermedius*. Struve's (1962) description and illustrations were of rather incomplete material and a detailed comparison is not possible; however, the glabellar furrowing and apparently larger, more posteriorly placed eye in *O. henningsmoeni* suggest that the two forms are distinct.

The species is distinguished from all other *Ogyginus* species by the small eye situated well forward, and a glabella encroaching onto the anterior border. Isolate pygidia with nine ribs are very difficult to distinguish from nine-rib forms of *O. corndensis*, though the short furrow on the distal portion of the anterior ribs in *O. intermedius* may be utilized if compression is not too great. For a fuller comparison with related species see the discussion of *O. corndensis* (p. 135) and Whittard (1964 : 253).

***Ogyginus* cf. *intermedius* Elles, 1940**
(Fig. 177)

Figured specimen. It.2890, internal mould of pygidium.

Locality and horizon. *Didymograptus bifidus* Shales, left bank of the stream section in the upper reaches of the Camnant Brook, 270 yd (247 m) below the fence crossing the stream above the ravine.

Description. This pygidium is very similar to pygidia here attributed to *O. intermedius*, except that the doublure is considerably wider, the width being slightly over one-quarter of the total pygidial length.

Discussion. It has been shown that in the closely-related species *O. corndensis* the relative width of the doublure is dependent on the size of the individual and increases with increase in size. Since this specimen is no larger than specimens of *O. intermedius* from the same locality, the wider doublure would seem to indicate a significant difference between this specimen and *O. intermedius*.

Ogyginus*? *laticostatus (Salter, 1866)
(Fig. 109)

1851 *Isotelus* (*Basilicus*) ? *laticostatus* (Green sp.); Sedgwick & M'Coy (*pars*) : 170; pl. 1E, fig. 18a only (*non laticostatus* of Green, 1832).
1852 *Isotelus laticostatus* (Green sp.); Sedgwick & M'Coy : 366.
1866 *Asaphus* (*Basilicus*) *laticostatus* Sedgwick & M'Coy; Salter : 158–159; pl. 18, fig. 6.
1931 *Ogyginus* ? *laticostatus* (McCoy); Reed : 462.
1953 '*Asaphus*' *laticostatus* M'Coy; Jaanusson : 445.

Holotype. SM A16693, internal mould of large pygidium. Holotype by monotypy.

Locality and horizon. This specimen was originally cited as having been collected from Maen Goran, Llangollen (Sedgwick & M'Coy 1851 : 170). Subsequently (Salter 1866 : 159; 1866*a* : 311–312) stated that it was from Maen Goran, Builth. No Maen Goran has been traced in either district, but there is a house named Maen Cowyn at Llanelwedd just north of Builth. This may be a modern spelling of Maen Goran (see note by G. L. Elles in the Sedgwick Museum Catalogue under the entry for the holotype); it might be noted, however, that Maen Cowyn was in use as early as 1894 (Woods 1894 : 572). Thus it is thought possible that the specimen came from near Maen Cowyn, possibly from the small track-side quarry, about 270 yd (247 m) west of Maen Cowyn, in ashy beds possibly of upper Llanvirn age.

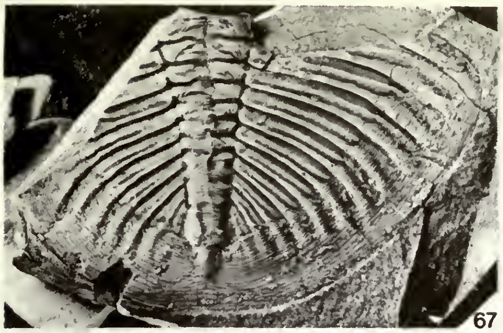
Description. Cephalon and thorax unknown.

Pygidium, though damaged, is roughly semicircular in outline. Axis slightly under one-quarter of pygidial width anteriorly, tapering posteriorly and defined by deep axial furrow. Exact number of axial rings uncertain but at least ten developed. Ring furrows continuous though very much shallower medially than laterally. At least nine, and possibly ten, flat-topped pleural ribs present. Doublure relatively narrow, being about one-seventh of the pygidial length in width. It appears to have a simple arcuate inner margin and bears terrace lines.

Discussion. If the location and age of this specimen are correct it represents the only occurrence of a trilobite from the upper Llanvirn in the southernmost part of the Inlier.

Figs 67, 69–70, 74. *Ogygiocarella debuchii* (Brongniart), p. 142. Fig. 67, Lower Llandeilo, old quarry 350 yd (320 m) west of Maesgwynne, SO 059566. Internal mould of pygidium, showing doublure and form of axial rings, It.2900, ×1·5. Figs 69–70, Lower Llandeilo, old quarry 570 yd (521 m) north of Wye Cottage, SO 047538. Fig. 69, internal mould of pygidium showing furrowing of axis, It.2904, ×2. Fig. 70, external mould of librigena with mould of dorsal surface of doublure and part of hypostoma, It.2911, ×1·5. Fig. 74, Lower Llandeilo, stream section 15 yd (14 m) SW of the old quarry 350 yd (320 m) west of Maesgwynne, SO 059566. Internal mould of damaged cranidium showing sculpture of fine ridges on glabella and occipital ring, It.2899, ×2·5.

Figs 68, 71–73, 75. *Ogyginus intermedius* Elles, p. 136. Figs 68, 75, Lower Llanvirn, right bank of upper reaches of Camnant Brook 175 yd (160 m) S 13° W of the fence crossing near the stream source, SO 088575. Fig. 68, internal mould of cranidium and part of thorax, showing glabellar furrows and scalloped nature of thoracic axial furrow, It.2887, ×1. Fig. 75, internal mould of pygidium showing irregular rib development, It.2886, ×1. Fig. 71, Lower Llanvirn, right bank of upper reaches of Camnant Brook 220 yd (201 m) S 13° W of the fence crossing near the stream source, SO 088575. Internal mould of small pygidium with an incipient tenth pleural rib developed, It.2884, ×7·5. Fig. 72, ? Lower Llanvirn, Frank's Bridge, Builth. Internal mould of complete large individual, SM A45484, ×0·5. Fig. 73, Lower Llanvirn, SE of Elusendy, Golden Grove, Llandeilo. Holotype. Internal mould of complete specimen, SM A10087, ×1.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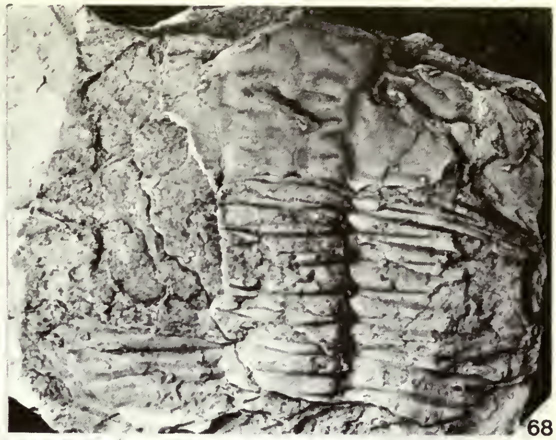
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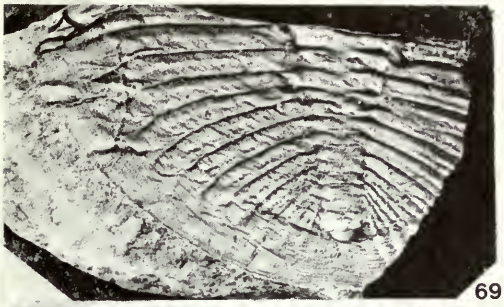
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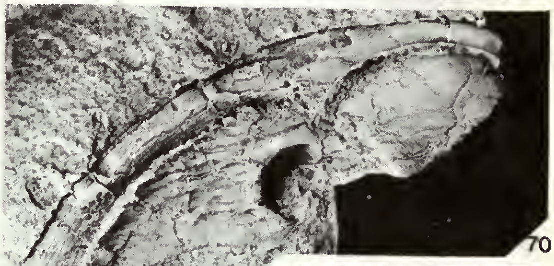
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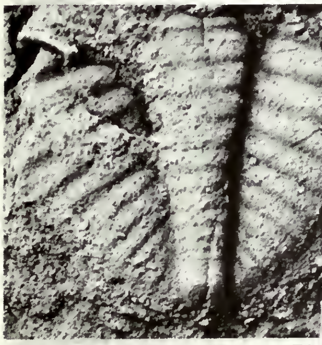
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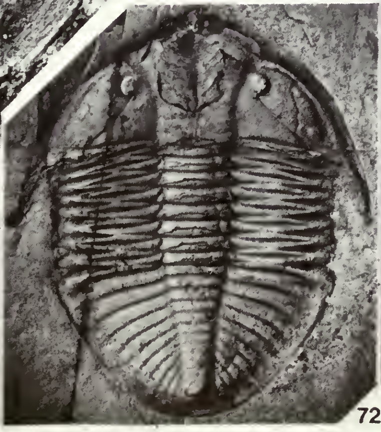
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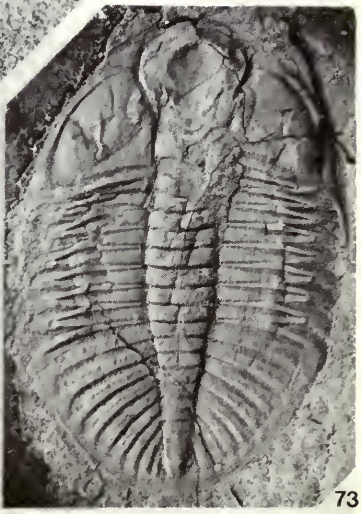
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Salter (1866 : 158–159; 1866*a* : 311–312) commented on M'Coy's inexplicable reference of this specimen to *Isotelus* (*Basilicus ?*) *laticostatus* Green, 1832, which Salter believed was in fact a phacopid, and indicated that the specimen clearly represented a distinct form with genuine asaphid affinities. Reed (1931 : 462) considered that the annulation of the axis, the relative width of the doublure and the nature of the pleural ribs indicated close affinity to *Ogyginus*, a suggestion also given some support by Jaanusson (1953 : 445–446). The specimen is very similar to large pygidia of *O. intermedius* and a tentative generic assignment to *Ogyginus* would seem the most plausible proposition. In view of the relatively poor preservation and the uncertainties regarding the age and locality of this specimen it is proposed that the species name should be retained but restricted to the holotype.

Genus ***OGYGIOCARELLA*** Harrington & Leanza, 1957

DIAGNOSIS. Outline oval, isopygous; cephalon and pygidium subsemicircular. Glabella parallel-sided posteriorly, expanding slightly frontally; four pairs of lateral glabellar furrows; eye situated in posterior half of cephalon; anterior branch of facial suture marginal frontally. Hypostoma with entire posterior margin. Thorax with scalloped axial furrow. Pygidium generally with 11 or more ribs and about 14 axial rings; inner edge of doublure sinuous.

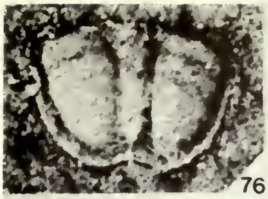
TYPE SPECIES. *Asaphus debuchii* (Brongniart, 1822). By original designation of Harrington & Leanza (1957 : 160–161), where it is misquoted as '*Asaphus debuchianus* (Brongniart, 1822)' (see Jaanusson *in* Moore 1959 : O352; Jaanusson 1956; Whittard 1964 : 255–256; Hughes 1972)[1].

DISTRIBUTION. Genus characteristic of the Anglo-Welsh region, particularly south Wales and Salop (Shropshire); only a single specimen is known from north Wales (MacGregor 1963 : 792–793). Also present in the Lower Llanvirn of Peru (Newell & Tafur 1944: pl. 92, figs 2–4; Hughes, Rickards & Williams in press).

DISCUSSION. Despite the reinterpretation of the course of the facial suture in *Ogyginus* (p. 124) the differences between *Ogygiocarella* and *Ogyginus* are few. However, the difference in facial suture pattern together with the greater expansion of the frontal glabellar lobe, the zetoidal axial furrow, the non-sinuate inner margin of the pygidial doublure and the generally lower number of pleural ribs in *Ogyginus* are considered to be sufficient to retain them as separate genera. *Ogygiocarella* also shows similarities to *Ogygiocaris* Angelin, 1854, but it may be distinguished by its marginal facial suture anteriorly, narrower cephalic doublure and lack of any posterior indentation in holaspides.

[1] For suppression of *Asaphus debuchianus* Brongniart *in* Desmarest, 1817, *non* 1822, see *Opin. Decl. int. Commn zool. Nom.*, London, **18** (4) : 241–256 (1958).

Figs 76–85. *Ogygiocarella debuchii* (Brongniart), p. 142. Figs 76–77, 82, Lower Llandeilo, stream section 15 yd (14 m) SW of the old quarry 350 yd (320 m) west of Maesgwynne, SO 059566. Fig. 76, latex impression from external mould of the smallest known transitory pygidium, It.2897, ×20. Fig. 77, internal mould of transitory pygidium showing at least three ribs, It.2896, ×20. Fig. 82, latex impression from external mould of meraspid of degree 4, It.2898, ×15. Fig. 78, Lower Llandeilo, 160 yd (146 m) SE of Tre Coed, on left bank of stream, SO 054552. Internal mould of transitory pygidium with eight ribs, It.2892, ×10. Figs 79, 81, 83–84, Lower Llandeilo, left bank of stream section east of Bach-y-graig, 45 yd (41 m) upstream of the point where the footpath enters the wood at the western end of the section, SO 071610. Figs 79, 83, internal mould of longitudinally compressed meraspid of degree 7, It.2913. Fig. 79, ×15; Fig. 83, ×10. Fig. 81, details of eye, It.2894, ×15. Fig. 84, internal mould of transversely compressed meraspid of degree 7, It.2893, ×10. Fig. 80, Lower Llandeilo, old quarry 570 yd (521 m) north of Wye Cottage, SO 047538. Internal mould of librigena and mould of ventral surface of doublure, It.2902, ×1·5. Fig. 85, Lower Llandeilo, stream section at Wellfield Lodge immediately above where the stream is piped under the road, SO 044528. Internal mould of young holaspis, It.2891, ×5.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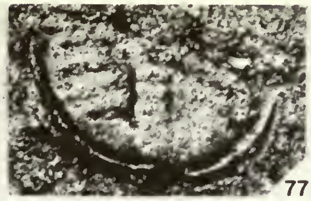
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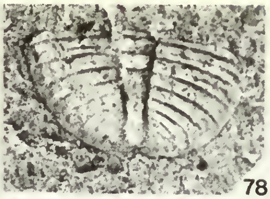
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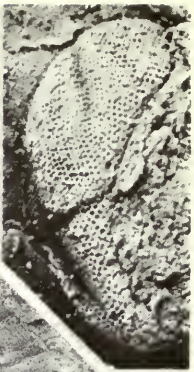
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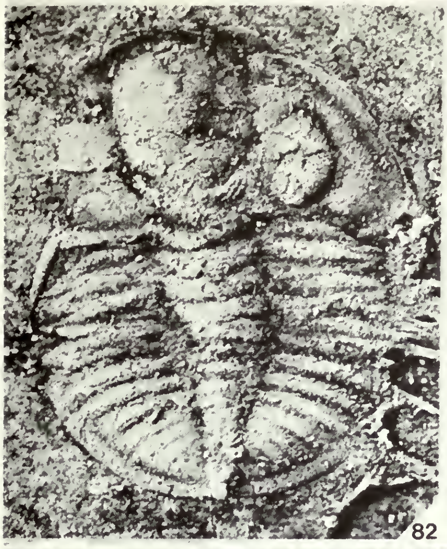
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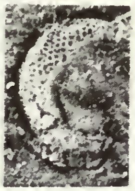
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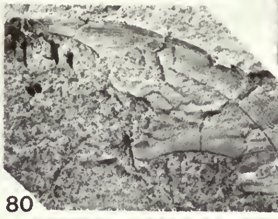
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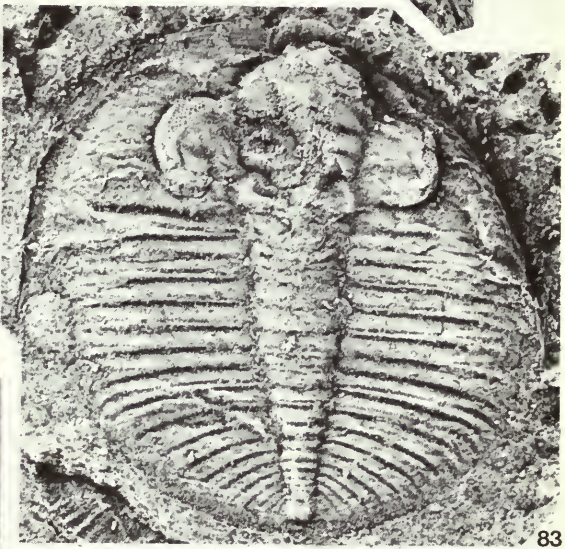
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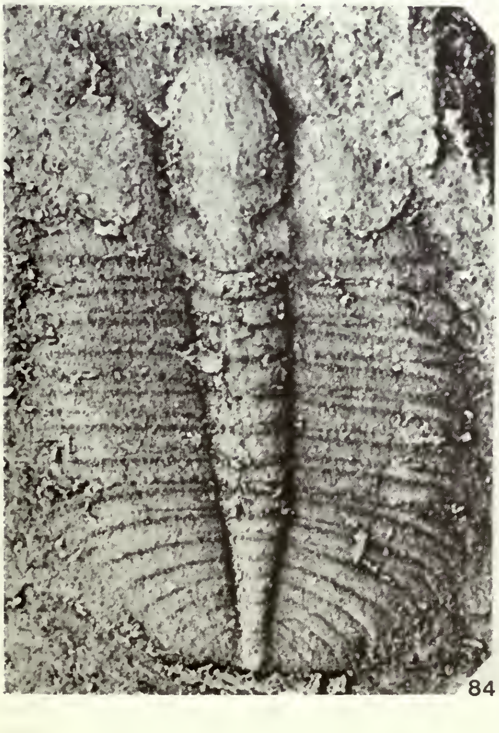
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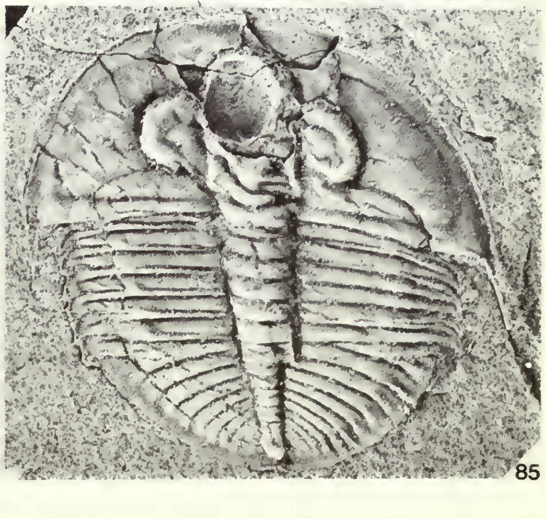
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Ogygiocarella debuchii (Brongniart, 1822)
(Figs 67, 69–70, 74, 76–86, 88–89, 91–92, 97)

1843 *Ogygia Buchii* (Brongniart); Goldfuss : 555.
1846 *Asaphus Buchii* Brongniart; De la Beche : 31.
1940 *Ogygiocaris buchi* (Brongniart) Elles (*pars*) : 406–412.
1964 *Ogygiocarella debuchii* (Brongniart); Whittard : 255–261; pl. 44, figs 1–11; pl. 45, figs 1–8 (includes fuller synonymy).
1966 *Ogygiocarella debuchii* (Brongniart); Whittard : 302.
1970 *Ogygiocarella debuchii* (Brongniart); Toghill : 122.
1972 *Ogygiocarella debuchii* (Brongniart); Hughes : 7–17.

DIAGNOSIS. *Ogygiocarella* generally having eleven pygidial ribs, rarely ten or twelve.

LECTOTYPE. Whittard (1964 : 261) selected as lectotype the specimen on which Brongniart (1822) based his plate 2, fig. 2A. This was unsatisfactory since the whereabouts of this specimen was, and is still, unknown. Nevertheless, it is proposed to accept Whittard's designation in order to preserve current usage of the name *O. debuchii* (see also Whittard 1964 : 256; Hughes 1972).

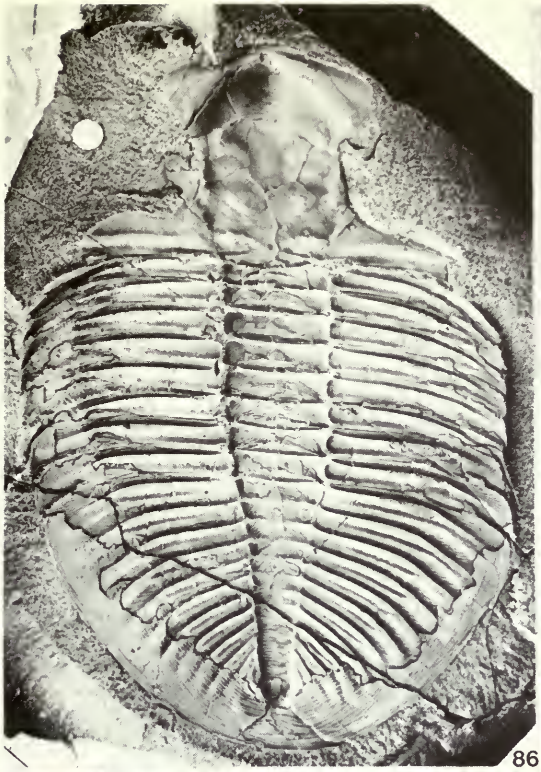
DISTRIBUTION. The species is common throughout much of south and central Wales and Salop (Shropshire), although some differences in stratigraphical range occur in different areas. The species first occurs near the top of the upper Llanvirn of the Builth district. De la Beche (1846 : 31) reported the species from the Grey Feldspar Sands at Tan-y-graig at a horizon somewhat lower than this, but no specimens have been located in substantiation. It persists until just below the top of the lower Llandeilo. In Salop it does not appear until the upper part of the lower Llandeilo (upper part of the Meadowtown Beds) and continues into the upper Llandeilo (Rorrington Beds), while in the Llandeilo region the species appears to be restricted to the Llandeilo. Numerous occurrences of the species have also been recorded from south Wales, but until the trilobites of this region are revised there is some doubt as to whether they can all be referred to *O. debuchii*, though it is certainly present in the Hendre Shales at Mydrim (Toghill 1970 : 122).

DESCRIPTION. The following descriptive notes supplement Whittard's (1964 : 257–261) description. Complete individuals are oval in outline being about one and a half times longer than wide. Some variation occurs in length/width ratio, but there is no evidence of the existence of distinct wide and narrow forms (Fig. 101) as claimed by Whittard (1964 : 257).

Cephalon approximately two and a half times as wide as long. In uncompressed specimens, unfurrowed frontal portion of the glabella moderately convex (*tr.*) with steep convex frontal face (cf. 59207, Fig. 86; SM A49721). Total length of glabella and occipital ring about one and three-quarters that of maximum glabellar width. Palpebral lobe situated entirely in posterior half of cephalon, mid-point being only about one-third of cephalic length from posterior margin. Eye moderately large, with all lenses approximately equal in size and hexagonal in outline. A relatively small specimen (eye length 3·0 mm) has visual surface with approximately 1000

Figs 86, 88–89, 91–92. *Ogygiocarella debuchii* (Brongniart), above. Fig. 86, unknown loc. in the Builth district. External mould of specimen lacking librigenae, 59207, ×1. Fig. 88, ? Llandeilo, loc. unknown but probably from the Llandeilo district. Internal mould of complete specimen showing well-developed nodes on the thoracic and pygidial axis, GSM 12880, ×1. Figs 89, 92, Lower Llandeilo, old quarry 570 yd (521 m) north of Wye Cottage, SO 047538. Fig. 89, internal mould of pygidium with twelve ribs, It.2908, ×1·5. Fig. 92, details of eye lenses, It.2910, ×10. Fig. 91, Lower Llandeilo, left bank of stream section east of Bach-y-graig, 20 yd (18 m) upstream of the point where the footpath enters the wood at the western end of the section, SO 072610. Internal mould of cephalon and part of thorax prepared to reveal mould of ventral surface of hypostoma, It.2895, ×2.

Figs 87, 90. *Ogygiocarella angustissima* (Salter), p. 150. Fig. 87, Middle-upper Llandeilo, quarry at Gwern-yfed-fâch, ½ ml (805 m) SE of Builth Road station, SO 030526. Internal mould of small pygidium with a slight posterior indentation, It.2923, ×7. Fig. 90, Middle-upper Llandeilo, middle quarry, Llanfawr, Llandrindod, SO 066617. Mould of dorsal surface of hypostoma, It.2917, ×3.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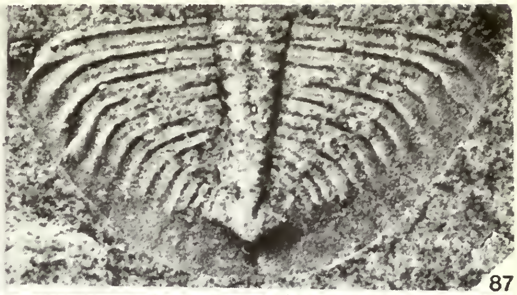
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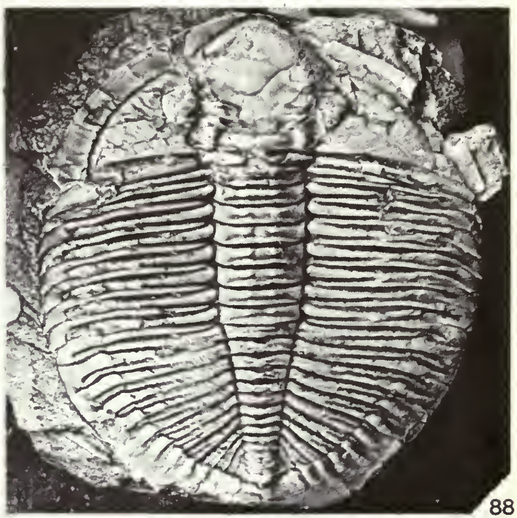
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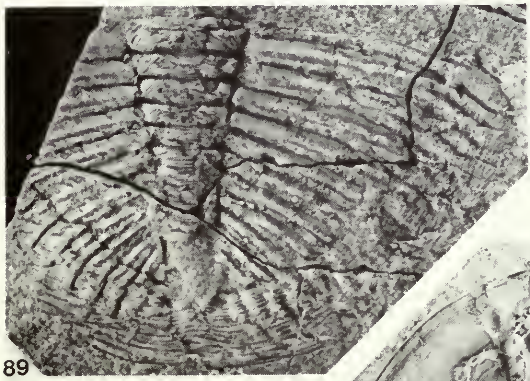
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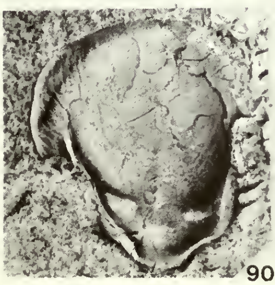
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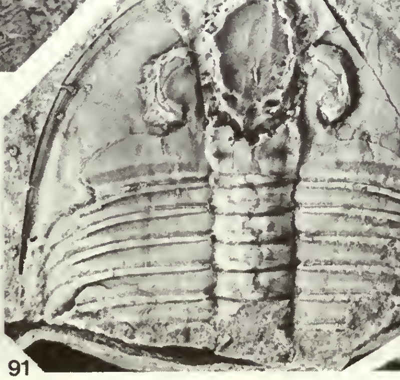
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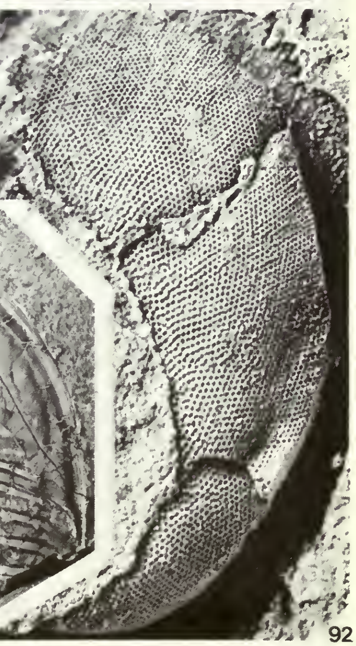
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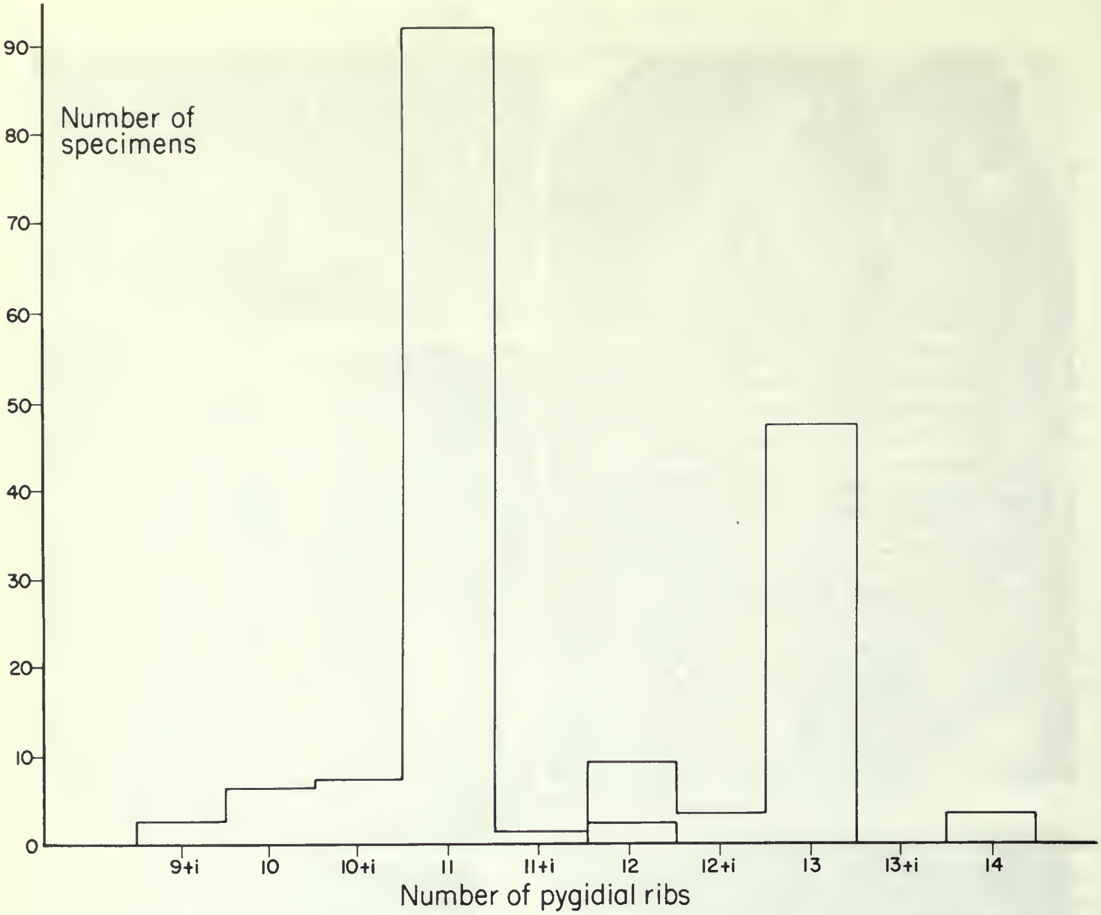

Fig. 93. Histogram of the number of pygidial ribs developed in *Ogygiocarella debuchii* (Brongniart) (left peak) and *Ogygiocarella angustissima* (Salter) (right peak).

lenses of about 0·033 mm diameter (Fig. 81). A larger specimen (eye length 8·5 mm) has approximately 4000 lenses of 0·055 mm diameter (Fig. 92). Visual surface approximately crescentic in outline, appearing to be widest anteriorly in dorsal view owing to the steeper inclination of the visual surface posteriorly.

External surface of frontal glabellar lobe bears a Bertillon pattern of fine, closely-spaced ridges (Figs 74, 86). Similar ridges are also present medially on posterior of glabella and occipital

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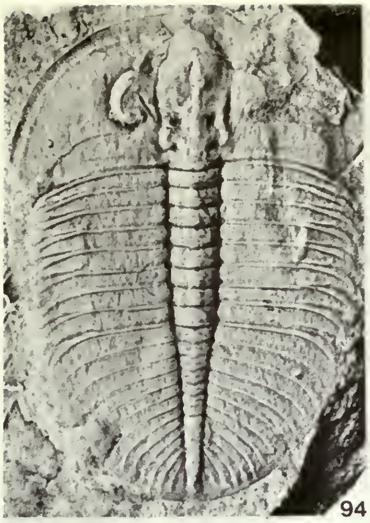
Figs 94–96, 98–100. *Ogygiocarella angustissima* (Salter), p. 150. Figs 94–95, Middle-upper Llandeilo, loc. uncertain (see p. 151). Fig. 94, **Lectotype.** Internal mould, 59198, ×2. Fig. 95, Paralectotype. Internal mould showing glabellar furrowing, 59199a, ×1·5. Figs 96, 100, Middle-upper Llandeilo, middle quarry, Llanfawr, Llandrindod, SO 066617. Fig. 96, part of cephalic doublure, showing possible panderian node near posterior margin, It.2919, ×3. Fig. 100, external mould of pygidial fragment showing surface sculpture, It.2914, ×3. Fig. 98, ? Middle-upper Llandeilo, loc. unknown but in the Builth district. Internal mould of virtually complete specimen having fourteen pygidial ribs, OUM B.123, ×1 (figured as *Asaphus debuchii* by Brongniart 1822: pl. 2, fig. 2c). Fig. 99, Middle-upper Llandeilo, ? quarry at Gwern-yfed-fâch, $\frac{1}{2}$ ml (805 m) SE of Builth Road station, SO 030526. Internal mould of large pygidium and posterior part of thorax, showing sinuate inner edge of pygidial doublure, I.2857b, ×$\frac{2}{3}$.

Fig. 97. *Ogygiocarella debuchii* (Brongniart), p. 142. Lower Llandeilo, old quarry 570 yd (521 m) north of Wye Cottage, SO 047538. Internal mould of relatively narrow pygidium, It.2906, ×1.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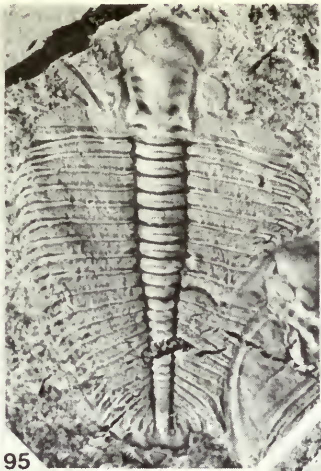
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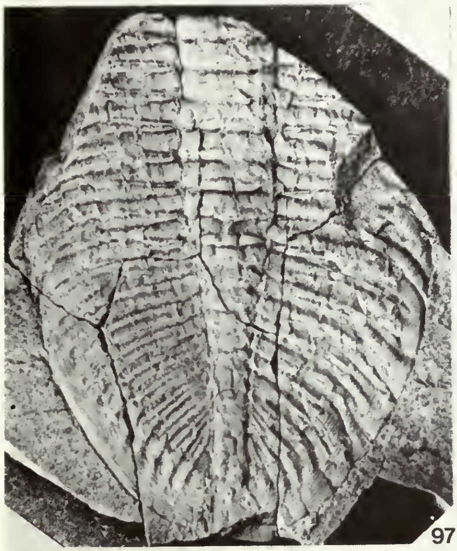
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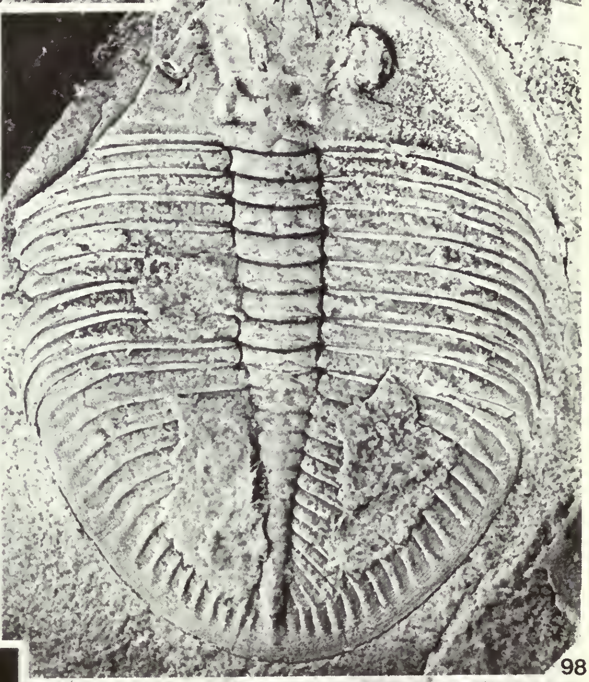
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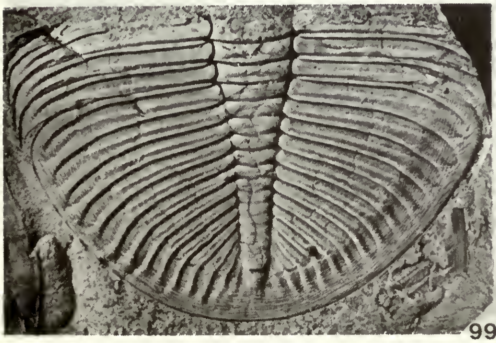
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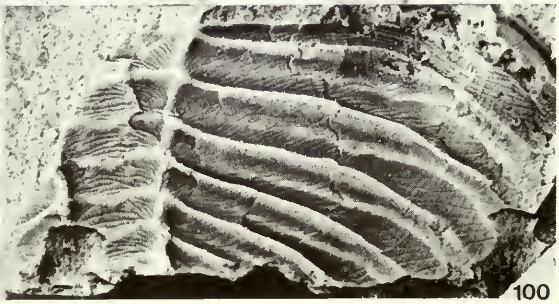
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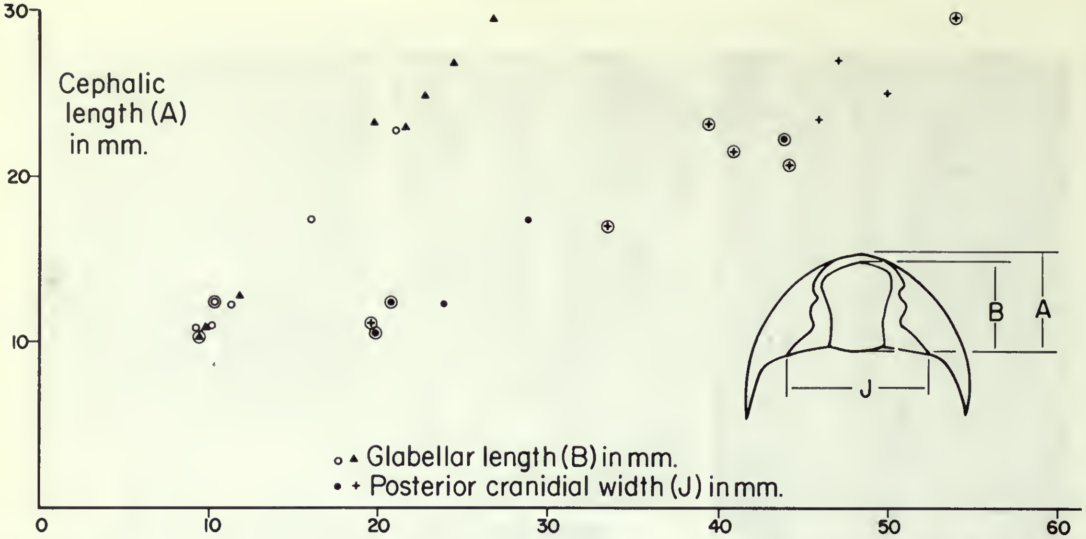

Fig. 101. Plots showing similarities between the cephalic dimensions of *Ogygiocarella debuchii* (Brongniart) (● ○) and *Ogygiocarella angustissima* (Salter) (+ ▲). Points enclosed by a circle are approximate.

ring (Fig. 74); here, however, they are not so markedly convex forwards. Remaining portions of dorsal cephalic exoskeleton smooth. Doublure moderately wide, though narrower anteriorly owing to location of hypostoma, and bearing fine terrace lines.

Thorax tapering slightly posteriorly. Axial furrows also converge slightly posteriorly. Nodes on axial rings occasionally developed in the Builth material; the only specimen known with these fully developed is GSM 12880, probably from Llandeilo (Fig. 88). No panderian openings or protuberances developed.

Pygidial axis infundibular, occupying slightly over one-sixth of pygidial width anteriorly and with up to 13 axial rings (rather than the 14 mentioned by Whittard), plus terminal piece. Generally, however, only between seven and nine axial rings are clearly differentiated, with little trace of furrowing on posterior of axis. Posteriorly apodemal pits in axial furrow become progressively less pronounced, disappearing at about the eighth or ninth axial ring. Typically eleven well-developed ribs present (see Table 11, p. 150). Posterior band of ribs is more convex (*exsag.*) than anterior one and distal to paradoublural line; ribs are deflected slightly more to the rear, this becoming progressively less posteriorly. Externally posterior bands bear raised lines lying oblique to interpleural furrows; distally these lines become subparallel to the margin

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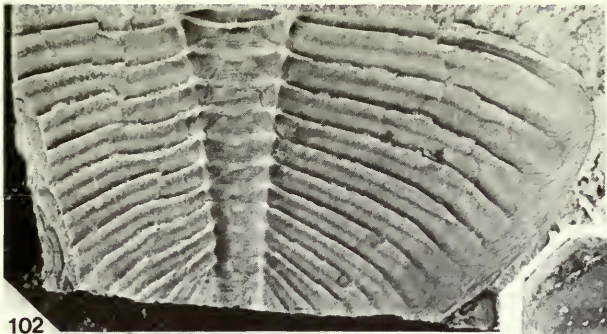
Figs 102–108, 110. *Ogygiocarella angustissima* (Salter), p. 150. Figs 102–103, 105–107, Middle-upper Llandeilo, middle quarry, Llanfawr, Llandrindod, SO 066617. Fig. 102, external mould of pygidium showing apodemal pits, It.2921, ×2. Fig. 103, latex impression from external mould showing sculpture, form of occipital ring, fixigenae and palpebral lobes, It.2918, ×2. Fig. 105, internal mould of eye showing traces of eye lenses, It.2920, ×10. Fig. 106, internal mould of damaged librigena showing sculpture and median suture, It.2915, ×3. Fig. 107, internal mould of part of thoracic segment, showing form and sculpture of the thoracic doublure, It.2916, ×2. Figs 104, 110, Middle-upper Llandeilo, quarry at Gwern-yfed-fâch, $\frac{1}{2}$ ml (805 m) SE of Builth Road station, SO 030526. Fig. 104, internal mould of librigena showing sculpture of cephalic doublure, It.2922, ×7. Fig. 110, external mould showing slight irregularity in the eighth rib on the left pleural field, 59206, ×0·5. Fig. 108, Middle-upper Llandeilo, ? Harper's quarry, NE of Wellfield, SO 038532. Internal mould of nearly complete specimen showing general form and position of the hypostoma, GSM 12918, ×1.

Fig. 109. *Ogyginus* ? *laticostatus* (Salter), p. 138. ? Upper Llanvirn, 'Maen Goran, Builth'; ? small quarry about 270 yd (247 m) west of Maen Cowyn, SO 054525 (see p. 138). Internal mould of pygidium, SM A16693, ×1.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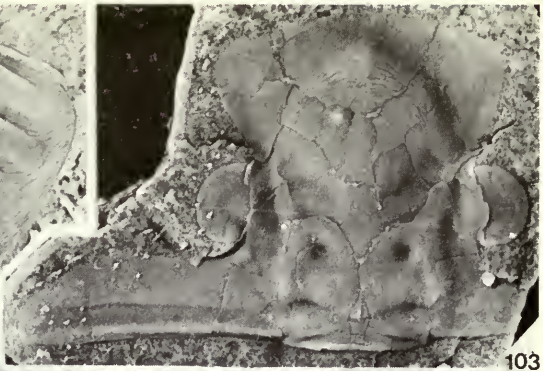
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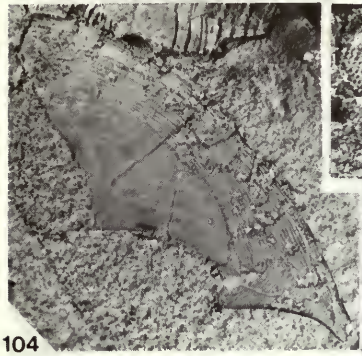
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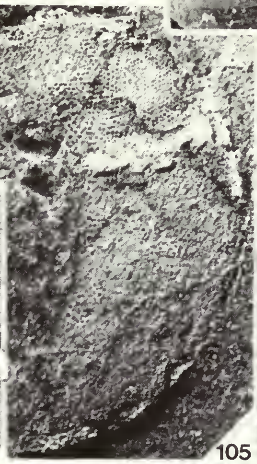
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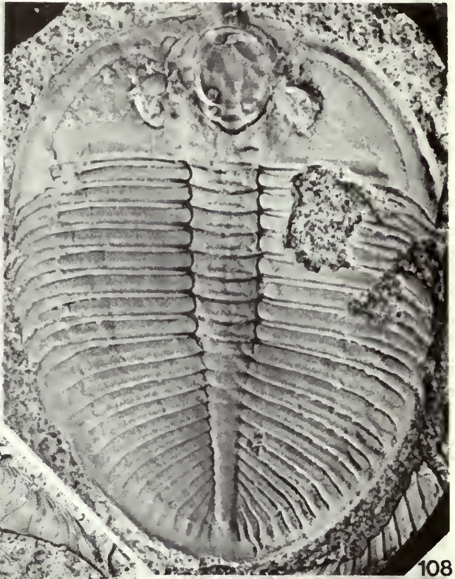
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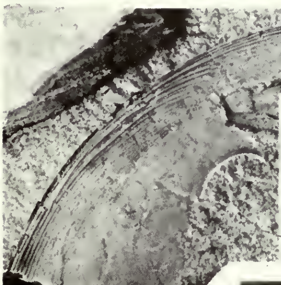
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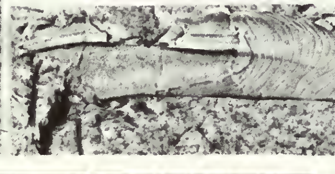
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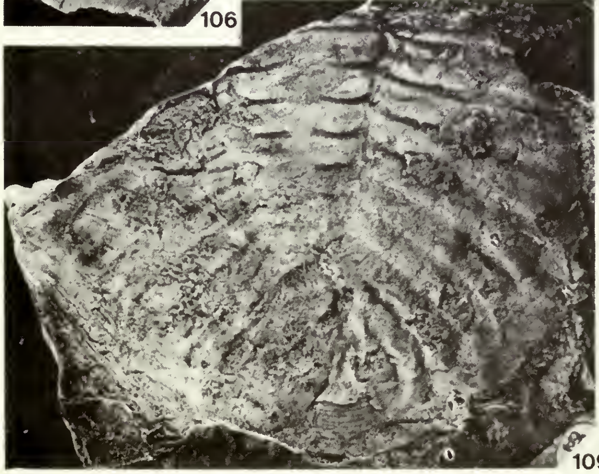
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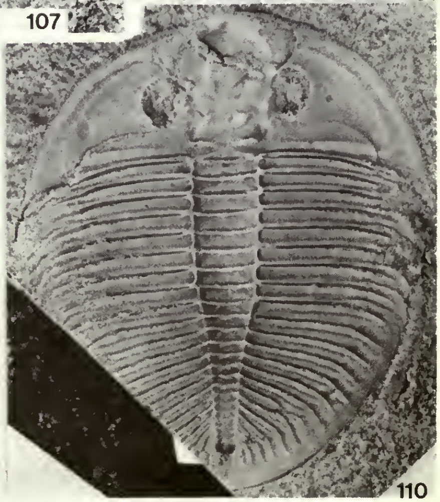
110

and extend onto the distal extremities of anterior bands (Fig. 86). Strong terrace lines developed on doublure subparallel to margins, becoming bunched together in post-axial region (Fig. 86).

ONTOGENY. Although only a few meraspid specimens are known from the Builth region, they show some interesting differences from the ontogenetic series described by Whittard (1964: 259–260) from the Shelve region. The Builth material consists of one entire specimen of degree 4 and two of degree 7, together with a few isolated transitory pygidia of uncertain degree.

Isolated transitory pygidia. Smallest known specimen, It.2897 (Fig. 76) is 1·3 mm wide and 0·8 mm long, roughly semicircular, globose, with a prominent posterior indentation. At least two ribs are present on anterior part of pleural field. Axial region approximately parallel-sided and weakly furrowed. Posterior and lateral borders well developed and flat. It.2896 (Fig. 77), width and length 1·6 mm and 0·8 mm respectively, is very similar but has at least three ribs developed. It.2892 (Fig. 78), 3·0 mm wide and 1·7 mm long, has eight ribs, the anterior ones having well-developed furrows along their entire length (*tr.*). The development of eight ribs would suggest, by comparison with Whittard's ontogenetic series, degree 3 or 4, but the well-developed pleural furrows are more characteristic of his degree 7 specimens.

Degree 4. Single known specimen, It.2898 (Fig. 82) is about 4·0 mm long. Cephalon not well preserved axially, but occipital ring appears simple, bowed posteriorly with continuous occipital furrow and no lateral occipital lobes. Basal pair of lateral glabellar furrows well developed. Eye large, almost half the cephalic length, with relatively few (up to 100) large lenses.

Thorax slightly disarticulated, but appears to consist of only four segments, similar to those of holaspides but with relatively deeper pleural furrows.

Transitory pygidium semielliptical, nearly three times as wide as long. Seven unfurrowed ribs developed. Axis with at least six axial rings and extending close to indented posterior margin.

Degree 7. Two entire specimens are 6·5 mm and 8·2 mm long (see Table 5).

Although basically similar to holaspides, the cephalon differs in various ways. Occipital ring simple with continuous furrow and no lateral occipital lobes. Glabella progressively expands slightly anteriorly and has only three pairs of lateral glabellar furrows, the anterior pair of the adult being absent. Eye still relatively large, being only just under half the cephalic length. Posterior border furrow dies out distally approximately in line (*exsag.*) with the fulcrum. As in holaspides, genal spine relatively short, reaching only to fourth thoracic segment.

The seven thoracic segments are as in holaspides.

Transitory pygidium semielliptical, with 9–11 ribs which may be shallowly furrowed along their entire length (*tr.*) (Fig. 83). Ribs deflected slightly posteriorly on reaching paradoublural line. Axis infundibular with ten axial rings and a terminal piece. No posterior indentation developed.

Apart from being slightly larger, specimen It.2893 (Fig. 84) is similar.

Table 5. Measurements and rib counts on meraspid specimens of *Ogygiocarella debuchii* (Brongniart). All measurements in mm. For explanation of symbols see Fig. 1.

Specimen	T.L.	A	W	Z	Ribs	Degree
It.2897	–	–	1·3	0·8	2+ ?	?
It.2896	–	–	1·6	0·8	3	?
It.2892	–	–	3·0	1·7	8	?
It.2898	*c.* 4·0	*c.* 2·0	3·0	*c.* 1·1	7	4
It.2913	6·5	2·9	5·2	1·9	9	7
It.2893	8·2	3·3	4·7	2·2	7+	7

DISCUSSION OF ONTOGENY. The series described by Whittard shows that transitory pygidia of degree 1 probably had six ribs and suggests that degree 0 transitory pygidia possessed fewer. The present study, however, has revealed meraspid transitory pygidia with only two or three ribs developed. Whether these are of degree 0 or not cannot be ascertained. Their size and the number of ribs developed would suggest that they are earlier than degree 4, but more likely to be of degree 2 or 3 than 0 or 1. The present study also shows that variations in the number of ribs developed at a particular degree do occur.

A striking difference between the Builth and Shelve meraspides is that of size, the Builth specimens being generally much smaller. Table 6 gives the comparative data for specimens from the two areas. As in the holaspid form, variations in the overall length/width ratios are known in the meraspides (Figs 83, 84; Whittard 1964 : pl. 45, figs 6, 7), although much of this variation results from *post-mortem* deformation.

Table 6. Comparative data for meraspid specimens of *Ogygiocarella debuchii* (Brongniart) from the Builth and Shelve regions. Column headed 'Locality' gives an indication of which specimens are from the same locality as others. All measurements in mm. * indicates a further incipient rib developed. For explanation of symbols see Fig. 1.

Builth						
Specimen	Degree	T.L.	A	Z	Ribs	Locality
It.2897	?	–	–	0·8	2+ ?	A
It.2896	?	–	–	0·8	3	A
It.2898	4	*c.* 4·0	*c.* 2·0	*c.* 1·1	7	A
It.2892	?	–	–	1·7	8	B
It.2913	7	6·5	2·9	1·9	9	C
It.2893	7	8·2	3·3	2·2	7+	C
Shelve						
GSM 102160	1	–	–	1·3	6	1
GSM 102163	2	3·3	–	1·5	7*	2
GSM 102164	3	*c.* 4·0	–	1·6	7+	2
GSM 102165	4	6·4	3·0	2·2	9	3
GSM 102166	5	5·7	2·6	1·8	10	4
GSM 102167	7	14·5	–	2·8	10	3

BIOMETRICAL DATA. Despite the common occurrence of the species in the Builth district, relatively few measurements are possible owing to the damaged state of much of the available material. Pygidia have provided most of the available data; insufficient cephalic and thoracic data are available to allow any formal analysis. Measurements are given in certain cases to give some quantitative idea of the dimensions and variation of some features. For ease of comparison, various dimensions of *O. debuchii* and *O. angustissima* (p. 146) are plotted on Fig. 101. In the cases where bivariate analyses have been possible, they have been computed using the total measurable sample from the Builth inlier rather than the sample from any specific locality.

Table 7. Ratios of the maximum cephalic length (A), thoracic length (Q), maximum pygidial width (W) and pygidial length (Z) to the total length (T.L.) for *Ogygiocarella debuchii* (Brongniart).

Specimen	T.L.	A/T.L.	Q/T.L.	W/T.L.	Z/T.L.
NMW 68.376.G210	26·4	0·33	0·31	0·67	0·36
NMW 68.376.G211	33·5	0·33	0·32	0·67	0·35
NMW 68.376.G212	*c.* 35·5	*c.* 0·30	*c.* 0·31	*c.* 0·71	*c.* 0·39
NMW 68.376.G213	*c.* 36·0	*c.* 0·32	*c.* 0·32	*c.* 0·67	*c.* 0·36
NMW 68.376.G214	38·4	0·33	0·29	*c.* 0·71	0·38

Table 8. Cephalic measurements for *Ogygiocarella debuchii* (Brongniart). All measurements in mm. For explanation of symbols see Fig. 1.

Specimen	A	B	C_3	J	J_1	K
NMW 68.376.G215	10·7	9·5	–	*c.* 20·0	–	–
NMW 68.376.G211	11·0	10·0	–	–	–	5·6
NMW 68.376.G214	12·5	11·4	–	24·0	–	*c.* 6·0
NMW 68.376.G216	12·6	*c.* 10·5	4·4	*c.* 21·0	–	5·5
NMW 68.376.G217	17·5	16·2	–	29·0	16·8	9·4
NMW 68.376.G218	*c.* 22·3	–	–	44·0	–	–
NMW 68.376.G219	23·0	21·3	–	–	–	12·4
NMW 68.376.G220	–	*c.* 11.0	–	–	–	*c.* 6·0

Table 9. Bivariate statistics for the thorax and pygidium of *Ogygiocarella debuchii* (Brongniart). All measurements in mm. For explanation of symbols see Fig. 1.

x : y	$\bar{x}$	var. x	$\bar{y}$	var. y	r	r_e	α	var. α	a	var. a	n
Q : R_2	15·08	41·29	7·21	10·68	0·95	0·95	1·06	0·0156	0·51	0·0036	9
R_2 : R_3	7·87	12·79	6·72	8·94	1·00	1·00	0·98	0·0005	0·84	0·0004	6
W : Z	30·08	299·07	18·28	131·04	0·97	0·98	1·08	0·0025	0·66	0·0008	29
W : X	25·92	253·52	4·61	9·33	0·99	0·99	1·07	0·0007	–	–	24
Z : Y	14·52	83·82	12·07	54·16	1·00	1·00	0·97	0·0001	–	–	38
Z : X	14·55	96·65	4·35	8·47	0·97	0·97	0·99	0·0015	0·30	0·0001	39

Table 10. Thoracic measurements for *Ogygiocarella debuchii* (Brongniart). All measurements in mm. For explanation of symbols see Fig. 1.

Specimen	R_1	Q	Specimen	R_1	Q
NMW 68.376.G216	*c.* 23·0	9·8	NMW 68.376.G221	*c.* 33·0	14·0
NMW 68.376.G211	*c.* 24·0	10·8	It.2903	*c.* 44·0	23·2
NMW 68.376.G215	*c.* 24·5	10·9	NMW 68.376.G217	*c.* 53·6	23·8
NMW 68.376.G213	25·4	11·4	NMW 68.376.G222	*c.* 55·0	23·2
NMW 68.376.G214	31·2	11·2	NMW 68.376.G223	*c.* 61·0	24·0

Table 11. Frequency distribution of ribs on the pleural fields of *Ogygiocarella debuchii* (Brongniart). The suffix 'i' indicates the development of a further incipient rib. See also Fig. 93, p. 144).

Number of ribs	9i	10	10i	11	11i	12
Number of specimens	0	1	7	82	1	2

DISCUSSION. Under a variety of names, this is one of the most commonly cited species in British Ordovician palaeontological literature, being first figured by Lhuyd in 1698. The validity and authorship of the species has been the subject of much debate, the two most recent contributions being by Whittard (1964) and Hughes (1972).

Ogygiocarella angustissima (Salter, 1865–6)

(Figs 87, 90, 94–96, 98–100, 102–108, 110)

1846 *Ogygia Buchii* (Brongniart); Burmeister (*pars*) : 59–61.
1865 *Ogygia angustissima* Salter : pl. 14, figs 8–9 (figures only).
1866 *Ogygia angustissima* Salter: 129 (text).
1940 *Ogygia buchi* (Brongniart); Elles (*pars*) : 408, 411, 412, 414–419, 421– 433.
1964 *Ogygiocarella debuchii* (Brongniart) var. *angustissima* (Salter) Whittard : 261–262; pl. 45, fig. 9; pl. 26, fig. 1. Includes earlier synonymy.
1966 *Ogygiocarella debuchii* (Brongniart) var. *angustissima* (Salter); Whittard : 302.

DIAGNOSIS. *Ogygiocarella* with 12–14 ribs developed on pleural field, majority of individuals having 13.

LECTOTYPE (herein selected): 59198 (Fig. 94), internal mould of nearly complete individual. Dimensions (in mm): T.L., 33·5. A, 11·2. B, 10·0. C, 5·3. C_1, 2·1. C_2, 3·8. J, *c.* 19·8. K_1, *c.* 4·3. R_1, *c.* 22·0. R_2, 3·7. R_3, 3·1. R_4, *c.* 21·0. Q, 10·8. Q_1, 1·2. W, 19·7. X, 2·9. Y, 11·5. Z, 12·0. For explanation of symbols see Fig. 1. Both pleural fields have thirteen ribs and at least nine axial rings developed.

Paralectotypes: 59199a (Fig. 95), 59199b, internal moulds of nearly complete specimens, 59199a lacking librigenae.

TYPE LOCALITY AND HORIZON. Specimen 59198, here selected as lectotype, is labelled as coming from 'Llandeilo Flags, Gilwern' and was recorded as such by Salter in his original description (1866 : 129). However, the beds exposed at and around Gilwern are of uppermost lower Llanvirn age, whereas this species is characteristic of the highest lower Llandeilo to upper Llandeilo rocks of the Builth area. The lithology of the lectotype slab is unlike any found at Gilwern, but is similar to that of the *Nemagraptus gracilis* Shales of middle–upper Llandeilo age, and it seems likely that the specimen is either from the middle quarry, Llanfawr, Llandrindod, or possibly from Gwern-yfed-fâch quarry, near Builth Road. While it is accepted that the designation of a lectotype from uncertain locality leaves much to be desired, a similar problem over locality exists for the other syntypes (59199a, b); they are listed as from Gwern-fydd, but their lithology strongly suggests that they are from Harper's quarry, a quarter mile (402 m) north-west of Wellfield. Specimen 59198 has, therefore, been selected as lectotype as it is the most perfect of the three syntypes.

DISTRIBUTION. The species appears to be restricted to the high lower Llandeilo and middle to upper Llandeilo. Until the faunas of south Wales have been restudied little can be said about its occurrence south of Builth except that it has recently been recorded from the topmost Llandeilo Flags at Pant-yr-hendre and Llan quarries near Mydrim, Dyfed (Carmarthenshire) (Toghill 1970 : 122).

DESCRIPTION. Complete individuals oval in outline, about one and a half times as long as wide, but with some variation (see Table 12).

The cephalon is identical to that of *O. debuchii* except that the palpebral lobe may be slightly more anteriorly placed in larger specimens of *O. angustissima*, but insufficient data are available at present to confirm this quantitatively. Eye appears to be similar to that of *O. debuchii*; one specimen (eye length 6·0 mm) has *c.* 2500 lenses (Fig. 105).

Hypostoma apparently like that of *O. debuchii.*

Pygidium, although basically similar to that of *O. debuchii*, differs in some features. Outline tends to be parabolic, slightly longer relative to its width than in *O. debuchii*, except in small specimens (width less than 27 mm). Infundibular axis occupies about one-seventh of pygidial width anteriorly. Between 12 and 14 ribs may be developed on the pleural field, with over three-quarters of the specimens having 13 ribs (see Table 15 and Fig. 93). At least 14 axial rings may be developed, but generally only the anterior seven or eight are clearly discernible (as in *O. debuchii*). A comparison of the respective bivariate statistics for pygidial length and anterior axial width reveals that the pygidial axis of *O. angustissima* is narrower, with respect to pygidial length, than in *O. debuchii.* As in other asaphids, irregularities in the rib development are rare, only a single example being known in *O. angustissima* (Fig. 110). In all other features the pygidium appears to be identical to that of *O. debuchii*, with the exception that some small holaspid specimens show a slight posterior indentation (Fig. 87).

BIOMETRICAL DATA. Slightly more data are available for *O. angustissima* than for *O. debuchii*, and they are presented in a similar manner, some slight modifications being made to suit the extra data available.

Table 12. Ratios of the maximum cephalic length (A), thoracic length (Q), maximum pygidial width (W) and pygidial length (Z) to the total length (T.L.) for *Ogygiocarella angustissima* (Salter).

Specimen	T.L.	A/T.L.	Q/T.L.	W/T.L.	Z/T.L.
NMW 68.376.G224	*c.* 29·0	*c.* 0·34	–	*c.* 0·62	*c.* 0·34
BM 59198	33·5	0·33	0·32	0·58	0·36
SM A44685	38·6	0·32	0·31	–	0·39
BM I.8076	48·1	0·30	0·31	0·69	0·39
SM A44686	50·5	0·30	0·31	0·70	0·39
NMW 68.376.G225	54·0	0·30	0·32	0·61	0·38
BM I.59215	60·4	0·29	0·31	0·67	0·40
BM I.4381	65·0	0·32	–	0·78	0·39
BM I.1330	70·5	0·33	0·30	*c.* 0·63	0·37
GSM 12918	71·5	0·29	0·31	0·68	0·41
SM A44696	71·8	*c.* 0·28	0·32	–	0·39
BM 59211	83·4	0·30	0·31	0·69	0·39
BM 59202	88·0	0·31	0·30	0·65	0·40
OUM B123	96·8	0·29	0·29	0·65	0·40
SM A44714	101·9	0·30	0·29	0·64	0·40

Table 13. Cephalic measurements for *Ogygiocarella angustissima* (Salter). All measurements in mm. For explanation of symbols see Fig. 1.

Specimen	A	B	C_3	J	J_1	K_2
NMW 68.376.G226	10·4	*c.* 9·5	*c.* 4·1	–	–	–
BM 59198	11·2	10·0	3·8	*c.* 19·8	–	–
SM A44685	12·4	–	4·6	–	–	–
NMW 68.376.G227	13·0	11·9	*c.* 5·4	–	–	–
SM A44730	13·6	–	–	27·0	12·3	–
SM A44686	15·0	–	–	–	14·2	–
NMW 68.376.G228	17·3	–	–	*c.* 33·6	–	–
BM 59215	17·4	–	–	37·1	–	–
NMW 68.376.G229	20·7	–	–	*c.* 44·2	21·5	–
BM I.4381	20·7	–	7·9	44·2	–	–
NMW 68.376.G230	21·6	–	8·9	*c.* 41·0	18·4	–
BM I.1330	23·3	21·7	–	*c.* 39·5	–	–
NMW 68.376.G231	23·5	20·0	*c.* 6·5	46·0	–	–
BM 59211	25·2	23·0	*c.* 10·8	50·0	–	15·7
BM 59202	27·0	24·6	12·4	47·0	–	*c.* 14·0
BM 59203	29·0	26·5	–	61·3	–	–
OUM B123	29·6	27·0	–	*c.* 54·4	–	–
BM 59211	30·0	27·0	–	–	–	–
SM A44714	30·3	26·8	12·4	*c.* 58·5	*c.* 28·5	16·8
SM A44723	34·0	30·5	14·1	68·6	29·0	19·2

DISCUSSION. Apart from the number of pygidial ribs, the differences between *O. angustissima* and *O. debuchii* are slight. If samples of each form in the Builth region are considered, there is a clear distinction based on the pygidial rib counts, although both species include morphologically intermediate specimens. There is also a clear stratigraphical separation between the two species in the Builth region. In the Shelve Inlier the situation is not quite so straightforward, as the two forms have an overlapping stratigraphical range with both occurring in the uppermost lower Llandeilo. This suggests that the fossil record has preserved details of a stock undergoing speciation, with concomitant blurring of sharp distinctions between the two species.

Table 14. Bivariate statistics for *Ogygiocarella angustissima* (Salter). All measurements in mm. For explanation of symbols see Fig. 1.

x : y	$\bar{x}$	var. x	$\bar{y}$	var. y	r	r_c	α	var. α	a	var. a	n
A : B	25·10	51·48	22·64	41·89	1·00	1·00	1·00	0·0007	0·90	0·0006	11
R_1 : Q	49·34	435·01	21·29	74·70	0·98	0·98	0·96	0·0055	0·41	0·0011	8
Q : R_2	20·23	48·74	8·53	11·55	0·97	0·97	1·14	0·0044	0·49	0·0008	19
R_2 : R_3	8·48	10·96	7·32	7·87	0·99	0·99	0·98	0·0009	0·85	0·0007	20
R_4 : Q	54·80	175·52	23·71	27·80	0·96	0·96	0·92	0·0065	0·40	0·0012	11
W : Z	46·31	349·97	27·51	115·22	0·93	0·94	0·97	0·0039	0·57	0·0015	32
W : X	47·18	351·83	7·88	10·26	0·89	0·90	1·02	0·0056	0·17	0·0002	34
Z : Y	26·89	111·61	22·36	70·82	1·00	1·00	0·96	0·0002	0·80	0·0001	42
Z : X	26·54	112·58	7·25	9·61	0·95	0·96	1·06	0·0018	0·29	0·0001	54

Table 15. Frequency distribution of ribs on the pleural fields of *Ogygiocarella angustissima* (Salter). The suffix 'i' indicates the development of a further incipient rib. See also Fig. 93.

Number of ribs	12	12i	13	13i	14
Number of specimens	9	3	77	2	5

Ogygiocaridinid gen. et sp. indet.

(Fig. 12)

FIGURED SPECIMEN. It.2927, internal and external moulds of complete meraspid of degree 0.

LOCALITY AND HORIZON. Left bank of stream section east of Bach-y-graig, 40 yd (37 m) upstream of the point where the footpath enters the wood at the western end of the section; in *Glyptograptus teretiusculus* Shales.

DESCRIPTION. Exoskeleton apparently complete, oval in outline, being 1·4 mm long and 1·05 mm wide. Cephalon semicircular with no genal spines. Glabella parallel-sided; axial furrow deep. Glabellar furrows consist of two notch-like indentations on either side of glabella situated at one-third and two-thirds the way along the glabella. Occipital ring bowed backwards sagittally, occipital furrow continuous but deepest laterally. Posterior border and border furrow well defined. Genal region convex, with no eye. Facial suture may, however, be submarginal with the librigena, and with it the eye, missing.

Transitory pygidium semicircular and slightly smaller than cephalon, being 0·55 mm long. Axis well defined, occupying one-fifth of pygidial width anteriorly and tapering posteriorly to become parallel-sided over the posterior half. Two ribs occupy anterior half of the gently convex pleural fields. Number of axial rings developed cannot be determined.

DISCUSSION. The taxonomic placing of isolated occurrences of very early growth stages is difficult. Among the genera known in association with this specimen is *Barrandia*, but although the early ontogenetic stages of this genus are not known, the general characters of both the cephalon and transitory pygidium of this specimen are more akin to the ogygiocaridinids, and it would seem most likely to belong to either *Ogyginus corndensis* (Murchison) or *Ogygiocarella debuchii* (Brongniart), both species being known from the same locality.

The apparent lack of eyes is noteworthy, as relatively large, prominent eyes are present in degree 4 meraspides of both *O. debuchii* and *O. corndensis*. However, Evitt (1961) found that no visual surface is discernible in the protaspides of some asaphids, although its future position is indicated by the course of the facial suture.

Asaphid gen. et sp. indet.

(Fig. 112)

FIGURED SPECIMEN. It.2928, internal mould of glabella and part of left fixigena. Dimensions (in mm): B, 11·6. C_1, *c.* 3·8. C_2, 3·5. K_2, 8·0. For explanation of symbols see Fig. 1.

LOCALITY AND HORIZON. Gwern-yfed-fâch quarry, ½ml (805 m) south-east of Builth Road Station; *Nemagraptus gracilis* Shales.

DESCRIPTION. Glabella well defined, constricted at about one-fifth of its length, expanding slightly to just anterior of the palpebral lobe, obtusely rounded anteriorly. Three pairs of lateral glabellar furrows present. Posterior pair situated opposite the narrowest part of glabella and develops pits adaxially. Median pair moderately deep, curved posteromedially, situated at about half-way along glabella, and distally fail to reach axial furrow. Anterior pair situated opposite anterior of palpebral lobe, short, shallow and directed slightly anteromedially. Occipital furrow continuous, though central portion shallower and bowed posteriorly. Very little of fixigena preserved, but apparently postericr portion extends for some way laterally posterior to eye. Both posterior border and border furrow moderately well developed.

DISCUSSION. The affinities of this specimen are unknown, although it bears some similarity to *Nobiliasaphus powysensis* sp. nov. (see p. 117). However, the glabella furrowing, occipital ring and position of the eye serve to distinguish it from that species. Specimen I.1331, labelled as '*Ogygia* . . . from Gwernyfod', is probably closely related to this form.

Family **NILEIDAE** Angelin, 1854

Genus ***BARRANDIA*** M'Coy, 1849

DIAGNOSIS. Exoskeleton oval, depressed and subisopygous. Glabella smooth, expanded frontally; axial furrow shallow; fixigena narrow (*tr.*) posteriorly. Eye well developed; genal spine short. Thorax of eight segments; doublure extending beneath more than half pleural width. Pygidium subsemicircular to subelliptical with prominent, weakly furrowed, axis and generally smooth pleural field.

TYPE SPECIES. *Barrandia cordai* M'Coy, 1849.

DISTRIBUTION. The genus first occurs in the Lower Llanvirn of south Wales, Salop (Shropshire) and Pont Seiont, north Wales. In the Builth area it is restricted to the lower Llandeilo, a horizon at which it is unknown elsewhere. The record of *B. homfrayi* Hicks from the Lower Llanvirn at Builth (Elles 1940 : 395) is considered to be based on a misidentification. The genus has been recorded also from the mid-Ordovician of North America (Hintze 1953; Webb 1956). However, it is thought likely that the specimen referred to by Hintze belongs to *Aponileus* (see Hu 1963) and that those mentioned by Webb also belong to that or a related genus.

DISCUSSION. The assignment of *Barrandia* to the Nileidae rather than the Asaphidae has been subject to some debate (Reed 1931; Prantl & Přibyl 1949; Jaanusson *in* Moore 1959). New

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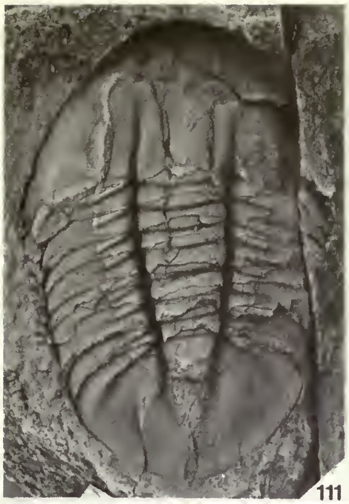
Figs 111, 114–119. *Barrandia cordai* M'Coy, p. 156. Fig. 111, Llandeilo, Builth, exact loc. unknown (see p. 156). Holotype. Internal mould of damaged specimen, SM A15626, ×2·5. Figs 114–119, Lower Llandeilo, left bank of Dulas Brook, 150 yd (137 m) SW of the old quarry 350 yd (320 m) west of Maesgwynne, SO 058564. Figs 114, 117, internal and external moulds of pygidium showing furrow separating parathoracic segment, It.2933, ×5. Fig. 115, internal mould of pygidium, It.2929, ×6. Fig. 116, internal mould of cranidium, It.2930, ×6. Fig. 118, internal mould of cranidium showing axial furrows fading out anteriorly, It.2931, ×6. Fig. 119, internal mould of pygidium with parathoracic segment, It.2932, ×6.

Fig. 112. Asaphid gen. et sp. indet., p. 153. Middle-upper Llandeilo, quarry at Gwern-yfed-fâch, ½ ml (805 m) SE of Builth Road station, SO 030538. Internal mould of glabella and part of left fixigena, It.2928, ×3.

Figs 113, 120–124. *Barrandia* cf. *cordai* M'Coy, p. 158. Figs 113, 120–122, 124, Lower Llandeilo, stream section 15 yd (14 m) SW of the old quarry 350 yd (320 m) west of Maesgwynne, SO 059566. Figs 113, 124, internal mould of entire specimen, It.2934. Fig. 113, enlargement of eye, ×10; Fig. 124, ×4. Fig. 120, external mould of transitory pygidium, showing weakly-developed ribs on the pleural fields, It.2939, ×8. Figs 121, 122, internal and external moulds of transitory pygidium, showing traces of two ribs, It.2938, ×6. Fig. 123, Lower Llandeilo, old quarry 350 yd (320 m) west of Maesgwynne, SO 059566. Internal mould showing cephalic doublure, It.2936, ×3.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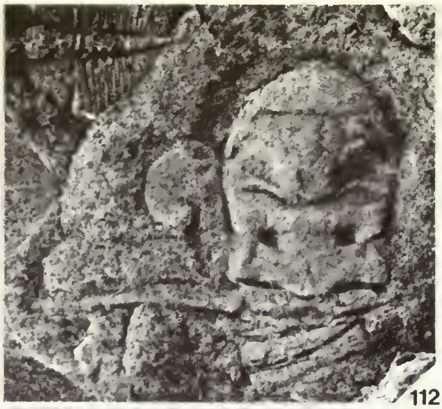
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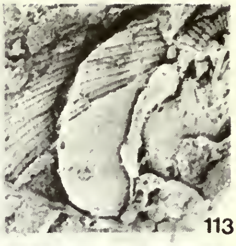
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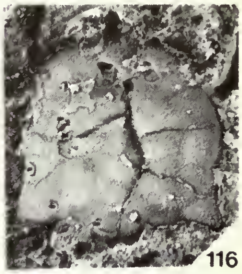
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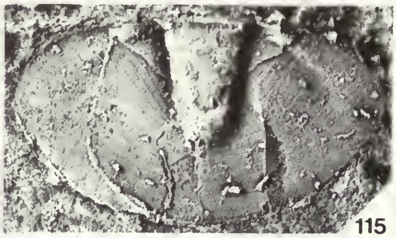
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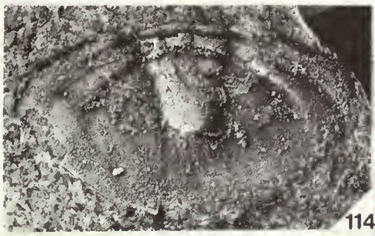
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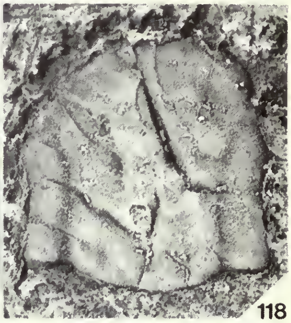
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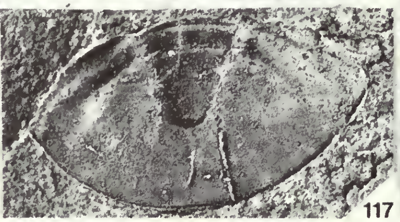
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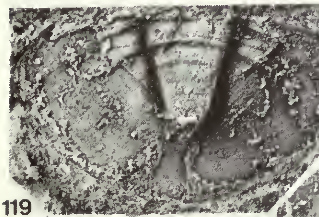
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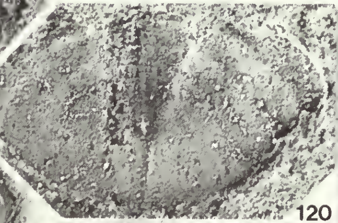
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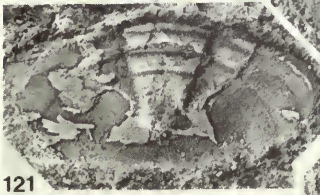
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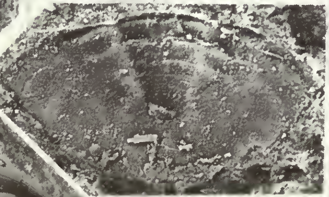
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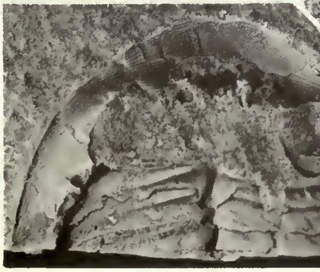
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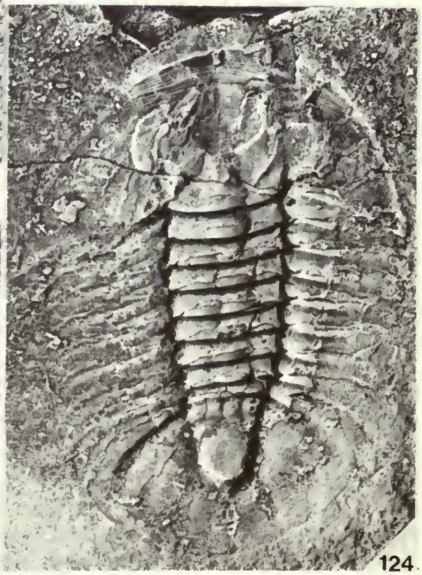

124

information regarding the nileids has recently become available (Fortey 1975) and it is believed that the general form of the exoskeleton, in particular that of the hypostoma (despite the presence of a furrow passing across the median body), cephalic doublure and eye, suggests that the assignment to the Nileidae is correct.

The eye-like 'nodular areas' described by Whittard (1961*a* : 221) are clearly seen in *Barrandia* and *Homalopteon* from the Builth area (Figs 113, 149), and have the concavo-convex outline characteristic of many trilobite compound eyes. Eye lenses in nileids are minute and commonly can only be seen with difficulty in well-preserved material (Fortey 1975). Despite the lack of visible lens structures in *Barrandia* and *Homalopteon* it is difficult to imagine these 'nodular areas' as anything but eyes.

The distinction between this genus and *Homalopteon* Salter is considered under the latter genus (p. 164). Owing to the common crushing and distortion of specimens, and also damage to, or complete loss of, the dorsal surface over the doublure, specific determinations are generally difficult. This applies particularly to *Barrandia* with its very wide doublure, although owing to the thin nature of the exoskeleton details of axial rings and pleural ribs are commonly distinguishable on both internal and external moulds; data from both have been included in the following specific descriptions. Systematic difficulties, especially assessments of variation, are further increased by the rareness of most species. Out of a total of fewer than 30 specimens from the Stapeley Shales, Whittard recognized five species based essentially on differences in the furrowing of the pygidial axis and pleural region. Some specific separations have been made in the present study on similar criteria, but it is possible that in both cases the differences may prove to be of an intraspecific nature.

Barrandia cordai M'Coy, 1849

(Figs 111, 114–119, 134)

1849 *Barrandia cordai* M'Coy; 409–410, text–fig.
1931 *Barrandia cordai* M'Coy; Reed : 443, 467 (gives earlier synonymy).
1940 *Barrandia cordai* M'Coy; Elles (*pars*) : 412.
1949 *Barrandia cordai* M'Coy; Prantl & Přibyl : 2, 4, 5, 14.
1961*a* *Barrandia cordai* M'Coy; Whittard : 221–223, 226–227; pl. 33, fig. 8.

DIAGNOSIS. *Barrandia* with subelliptical pygidium, having narrow conical axis with first two axial rings distinct; third and fourth indistinct; pleural field smooth apart from well-developed border furrow.

HOLOTYPE. SM A15626 (Fig. 111), internal mould of damaged entire individual. Dimensions (in mm): T.L., *c.* 25·0. A, *c.* 8·8. I, *c.* 17·0. J_2, *c.* 9·0. Q, *c.* 8·5. Q_1, 1·4. R_1, 15·5. R_2, 5·1. R_4, 13·2. R_5, 2·3. R_6, 2·0. W, 12·6. X, 3·2. Z, 7·7. Dimensions of hypostoma It.2948 (in mm): H_1, 8·2. H_4, 2·9. H_5, 7·7. H_6, *c.* 8·3. H_7, 7·0. H_8, 5·8. For explanation of symbols see Fig. 1.

TYPE LOCALITY AND HORIZON. The locality for the holotype was given by M'Coy (1849 : 410) as 'Black Wenlock shale of Builth'. Salter (1866 : 143) quotes it as from 'Penkerrig, near Builth, Radnorshire'. Elles (1940 : 412, 421) recorded the species from various localities which she believed to be of Llandeilo and basal Caradoc age; Whittard (1961*a* : 227), however, considered the species to be most likely of basal Caradoc age (basal *N. gracilis* Zone). Addison (*in* Williams *et al.* 1972 : 35–36) has shown that the basal portion of the *N. gracilis* Zone is of middle and upper Llandeilo age. The holotype is preserved in a dark greyish-blue shale which compares with both lower and middle to upper Llandeilo rocks of the Builth sequence. The present study indicates that *Homalopteon radians* (M'Coy) is the only nileid occurring at Pen-cerrig and that forms attributable to *B. cordai* are known only from the exposures in the left bank of the Dulas Brook, 150 yd (137 m) south-west of the old quarry 350 yd (320 m) west of Maesgwynne, and from the old quarry in the right bank of the stream 570 yd (521 m) north of Wye Cottage. Both these exposures are in *Glyptograptus teretiusculus* Shales of lower Llandeilo age.

DESCRIPTION. The holotype is the only complete specimen known. Its length is about one and a half times its maximum width.

Cephalon roughly semicircular, about one-third of the total length of the specimen. Glabella characteristically devoid of furrows, the two longitudinal furrows on the holotype being due to distortion, which, owing to the thin exoskeleton, is relatively common and may show a degree of symmetry in some specimens. Posteriorly the glabella occupies slightly over three-fifths of the cranidial width, anteriorly expanding in width to form the whole of the anterior part of the cranidium. Axial furrows shallow and subparallel posteriorly, becoming divergent and shallower anteriorly and fading out altogether before reaching lateral margins (Fig. 118). Fixigena a narrow flat band alongside the posterior two-thirds of the glabella, merging anteriorly with the expanded frontal region of the glabella. No discrete palpebral lobe developed and relatively little posterior expansion of the fixigena. Facial suture gently sigmoidal, being curved outwards in its anterior and posterior portion, becoming marginal anteriorly. Librigena subtriangular with a short genal spine. No median suture developed, and the librigenae form a single unit with the ventral doublure. The eye is not certainly known. The so-called eye previously described is thought to be an artefact resulting from imperfect preservation. Cephalic doublure poorly known, but anteriorly appears to have projections on the inner margin presumably surrounding the anterior wings of the hypostoma. Doublure bears a series of parallel terrace lines, at least 12 being present anteromedially in the holotype.

Hypostoma subrectangular with small anterior wing extending for about one-third of the hypostomal length. Lateral margins subparallel though slightly convex outwards. Posterior wing small, short (*sag.*); posterior margin protruded into a broad mesial tongue-like extension. Anterior lobe subcircular, much larger than posterior lobe, and bounded by a well-developed middle and lateral furrow; posterior lobe crescentic. Posterior border furrow well developed mesially, though shallower than middle furrow with which it merges anterolaterally. Maculae absent. Surface bears fine raised lines generally conforming in shape to that of the middle furrow; on the posterior border, however, they become modified to be subparallel to the posterior margin.

Eight thoracic segments are present as in other *Barrandia* spp., not seven as shown in Moore (1959 : O357, fig. 267.9). Axial rings simple, bowed gently posteriorly and with a well-developed articulating furrow. Anteriorly the axis occupies about two-fifths of thoracic width and tapers slightly to the rear. Axial furrow well incised and slightly zetoidal. Pleurae falcate, each having a strong diagonal furrow commencing at the inner anterior corner and fading out about halfway across the pleural region. Wide doublure underlies nearly two-thirds of pleural region and bears numerous outwardly concave terrace lines.

Pygidium subelliptical with anterior margin convex forwards. Axis relatively narrow and cone-shaped, occupying slightly under one-quarter of the anterior width and extending for about two-thirds of the pygidial length. In the holotype the axis is poorly preserved, but nevertheless shows a faint indication of one axial ring. It.2932 (Fig. 119) shows two distinct, and possibly up to four faintly-defined, axial rings and a terminal piece. This specimen, however, is small, and the furrowing may become lost in the larger individuals. Anterior border well developed, becoming shallower distally and failing to reach the lateral margins. Remainder of pleural field thought to be smooth, although owing to the common loss of the dorsal exoskeleton in this region it is difficult to be certain. Wide doublure underlies almost entire pleural region and

Table 16. Measurements for *Barrandia cordai* M'Coy. All measurements in mm. For explanation of symbols see Fig. 1.

Specimen	A	J	K_1	W	X	Y	Z
It.2929	–	–	–	8·0	1·9	2·5	4·3
It.2930	4·3	c. 4·7	2·8	–	–	–	–
It.2931	5·6	5·7	3·6	–	–	–	–
It.2932	–	–	–	7·7	2·0	2·1	3·7
It.2933	–	–	–	7·9	2·2	2·1	c. 4·2
NMW 68.376.G232	c. 5·7	–	3·5	–	–	–	–
NMW 68.376.G233	6·5	c. 7·0	4·3	–	–	–	–

bears fine terrace lines subparallel to the margins. Posteromesially about 15 terrace lines are present.

ONTOGENY. Two small pygidia similar to those of holaspides are known in which a ‘thoracic’ segment appears to be fused along the anterior margin (Figs 114, 117, 119). It.2933 (Fig. 117) does not show any furrow between the ‘thoracic’ segment and the rest of the pygidium on the external surface, but a clear furrow is impressed on the internal mould (Fig. 114), indicating a slight thickening of the exoskeleton along the line of junction. It is thought that both these specimens represent late meraspides with a parathoracic segment developed prior to release into the thorax. Fortey (1975 : 63) has shown that the release of the final segment in Nileidae may occur at a comparatively late stage in ontogeny. A meraspis of *B. ultima* sp. nov. (Fig. 130) shows two segments developed in the anterior part of a relatively large transitory pygidium. Unfortunately nothing more is known of the ontogenies of *Barrandia* species.

DISCUSSION. Previous descriptions of this species have been based on the holotype, which, although a relatively complete specimen, has certain crucial regions either missing or poorly preserved. Elles believed the species to be fairly widespread in all post-Llanvirn beds of the Builth region but did not give any redescription. The present study has shown that the species is rare in the Builth inlier.

B. cordai is distinguished from *B.* cf. *cordai* by its narrower pygidial axis and from *B. expansa* sp. nov. (p. 159) by the different outline of the pygidial axis. *B. ultima* sp. nov. (p. 160) has a better-developed cephalic axial furrow, relatively wider (*tr.*) fixigena and a greater number of axial rings on the pygidium. *B. homfrayi* Hicks, 1875 differs in having a relatively wide furrowed pygidial axis and a relatively wide cranidium. *B. tasgarensis* Whittard, 1961*a*, which is very similar to though narrower than *B. homfrayi*, is distinguished by the lack of furrows on the pygidial axis, while *B. bianularis* Whittard, 1961*a*, is readily distinguished by its relatively wide, stumpy pygidial axis with two clearly-defined axial rings. *B. parabolica* Whittard, 1961*a* is in many ways similar to *B. cordai*, but the marked parabolic outline of the cephalon and pygidium appears to distinguish Whittard's species. The hypostoma is similar to that described by Whittard (1961*a* : 223–224) in *B. homfrayi* but the anterior wing is more anteriorly placed and the posterior lobe narrower (*tr.*) in *B. cordai*.

***Barrandia* cf. *cordai* M'Coy**

(Figs. 113, 120–126)

DIMENSIONS (in mm): It.2934: T.L., *c.* 23·7. A, *c.* 7·5. I, *c.* 18·0. K_1, *c.* 5·6. Q, *c.* 8·8. Q_1, 1·3. R_1, *c.* 16·0. R_2, 5·3.

	W	X	Y	Z
It.2934	13·0	3·6	4·0	7·4
It.2935	10·5	3·0	3·2	5·5
It.2937	6·2	1·8	2·0	3·2
It.2938	6·7	1·9	2·2	–
It.2939	*c.* 6·0	1·5	*c.* 2·0	3·3

For explanation of symbols see Fig. 1.

LOCALITIES AND HORIZON. It.2935–6 are from the old quarry 350 yd (320 m) west of Maesgwynne, and It.2934, 2937–9 are from the stream section 15 yd (14 m) south-west of this quarry; both are in *Glyptograptus teretiusculus* Shales of lower Llandeilo age.

DESCRIPTION. It.2934–5 are very like *B. cordai*, except that the pygidial axis is somewhat broader and has a slightly expanded anterior portion similar to that of *B. expansa* sp. nov. It.2934 also shows one eye moderately well preserved, situated at about the mid-length of the cephalon, with a clear concavo-convex outline (Figs 113, 124). No lens structures are preserved.

It.2936 is the only other specimen of *Barrandia* known from the old quarry west of Maesgwynne and is included here. It shows the mesial portion of the cephalic doublure with about

16 subparallel terrace lines anteriorly, and the projection on the inner margin that abuts against the anterior wing of the hypostoma (Fig. 123).

ONTOGENY. Three smaller *Barrandia* pygidia from the stream section appear to have two well-developed axial rings and two pleural ribs. The ontogeny of *Barrandia* species suggests that these probably represent meraspides, rather than a small species characterized by a ribbed pleural field. Although an impression of the dorsal exoskeleton is absent in the pleural regions in both internal moulds and not well preserved in the external mould, traces of the two ribs are present axially (Figs 120–122), which, together with the two anterior axial rings, may make up parathoracic segments. The lateral extent of these ribs is not known; traces on the doublure in It.2937 suggest they continue to near the lateral margin, whereas in It.2939 they appear to die out rapidly with only the deeper anterior border furrow encroaching onto the wide border region. Wide doublure underlies most of pleural region, and bears terrace lines subparallel to pygidial margins.

DISCUSSION. The slightly wider axis in this form may be an expression of intraspecific variation present in *B. cordai*, but until more material is available it is best considered as a form closely related to *B. cordai*. If the small pygidia with two ribs are correctly assigned to the meraspid period they support the other evidence suggesting that the late retention of parathoracic segments is a characteristic of all *Barrandia* species.

Barrandia expansa sp. nov.

(Figs 127–129)

DIAGNOSIS. *Barrandia* with marked expansion of anterior portion of pygidial axis; pleural field with well-developed anterior border furrow; axis with two axial rings and large terminal piece.

NAME. 'Spread out'.

TYPE MATERIAL. Holotype It.2940 (Fig. 128), internal mould of pygidium. Paratypes, It.2941 (Fig. 127), external mould of thorax; It.2942 (Fig. 129), internal mould of pygidium.

DIMENSIONS (in mm):	Q_1	R_1	R_2	R_4	W	X	Y	Z
Holotype	–	–	–	–	*c.* 14·5	4·3	*c.* 4·0	7·3
It.2941	1·2	11·0	4·1	10·5	–	–	–	–
It.2942	–	–	–	–	*c.* 14·0	*c.* 4·0	*c.* 4·6	–

For explanation of symbols see Fig. 1.

LOCALITIES AND HORIZON. The holotype and It.2941 are from the left bank of the stream section east of Bach-y-graig, 45 yd (41 m) upstream of the point where the footpath enters the wood at the western end of the section. It.2942 is from the left bank of the stream section, 120 yd (109 m) south-east of Tre Coed. Both are in *Glyptograptus teretiusculus* Shales of lower Llandeilo age. The species is known with certainty only at these two localities.

DESCRIPTION. Cephalon unknown. Thoracic axial rings simple, with terrace lines on external surface. Pleurae falcate, with pleural furrow extending obliquely from the anterolateral corner towards the posterolateral corner, dying out just over one-third of the distance across the pleura at a point thought to coincide with the inner margin of the doublure. Dorsal surface bearing a series of fine, gently sigmoidal, raised lines in an anterolateral–posteromedian direction.

Pygidial axis slightly over half pygidial length, anteriorly occupying about three-tenths of greatest pygidial width. Axis funnel-shaped, with axial furrows converging posteriorly in the anterior half, becoming parallel-sided in posterior portion. Two well-developed axial rings present in the anterior tapering portion; posterior portion without furrows. Axis bears fine, transversely-directed, raised lines. Pleural field with well-developed anterior border furrow. Wide doublure underlies most of pleural field, and has terrace lines subparallel to pygidial margins.

DISCUSSION. Only the three figured specimens are known. Of other *Barrandia*, *B. expansa* appears to be most like *B. bianularis* Whittard, 1961*a*, but it is readily distinguished from this by its infundibular axis.

Barrandia ultima sp. nov.
(Figs 130–133, 135–136, 140)

1940 *Barrandia* (*Homalopteon*) *radians* (M'Coy); Elles (*pars*) : 412.

DIAGNOSIS. *Barrandia* having relatively well developed cephalic axial furrow reaching lateral cranidial margin. Pygidial axis with probably four axial rings and terminal piece; pleural field smooth apart from anterior border furrow.

NAME. 'Last'.

TYPE MATERIAL. Holotype, It.2945 (Fig. 136), internal mould of entire, but damaged, specimen. Paratypes, It.2943 (Fig. 135), internal mould of pygidium with parathoracic segment. It.2944 (Fig. 131), internal mould of cranidium. BU 455 (*ex* Chamberlain Collection 147/14) (Fig. 140), internal mould of damaged entire specimen.

DIMENSIONS (in mm). Holotype: T.L., *c.* 15·4. A, *c.* 5·8. I, *c.* 13·4. K_1, 3·9. Q, 5·2. Q_1, 0·8. R_1, *c.* 12·0. R_2, *c.* 3·5.

	W	X	Y	Z
Holotype	*c.* 9·0	2·4	2·5	4·4
It.2943	8·3	1·7	2·0	3·4
BU 455	9·7	2·5	3·0	5·0

For explanation of symbols see Fig. 1.

LOCALITY AND HORIZON. All type specimens are from the stream section 400 yd (365 m) north-east of Gorse, north-east of Llandrindod; *Glyptograptus teretiusculus* Shales of Lower Llandeilo age. Restricted to the type locality and to beds a little higher in the succession exposed about 20 yd (18 m) downstream from it.

DESCRIPTION. Similar to *B. cordai* and a comparative description only is required.

Complete individuals tend to be slightly wider than *B. cordai* having a length : width ratio of about 12 : 9 against 12 : 8 for *B. cordai*, but how flattening may have altered the original proportions is not known.

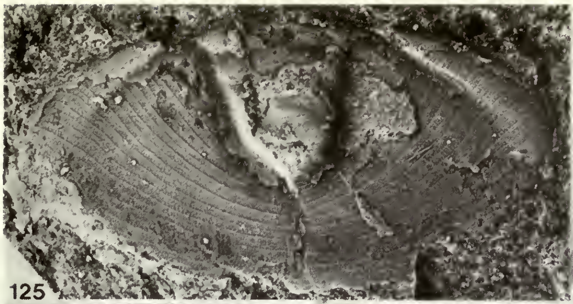
Cephalon differs from *B.* cordai in that the axial furrow is more strongly developed anteriorly and extends to the lateral cranidial margin, to cut it immediately anterior of δ, and the fixigena is slightly wider (*tr.*). Traces of the hypostoma are seen in It.2945 (Fig. 136), and it appears to conform to the general *Barrandia* pattern with large subcircular anterior lobe and a short (*sag.*) crescentic posterior lobe. Posterior margin protruded into a median lip and surface of median body bearing a series of subconcentric raised lines.

Figs 125–126. *Barrandia* cf. *cordai* M'Coy, p. 158. Lower Llandeilo, old quarry 350 yd (320 m) west of Maesgwynne, SO 059566. Internal and external moulds of pygidium showing wide, slightly forwardly expanding axis and transverse sculpture on dorsal surface, It.2935, ×6.

Figs 127–129. *Barrandia expansa* sp. nov., p. 159. Figs 127–128. Lower Llandeilo, left bank of stream section east of Bach-y-graig, 45 yd (41 m) upstream of the point where the footpath enters the wood at the western end of the section, SO 071610. Fig. 127, Paratype. External mould of thorax, It.2941, ×5. Fig. 128, **Holotype.** Internal mould of pygidium showing frontal expansion of axis, It.2940, ×4. Fig. 129, Lower Llandeilo, 120 yd (109 m) SE of Tre Coed on left bank of stream, SO 054552. Paratype. Internal mould of pygidium, It.2942, ×3·5.

Figs 130–133, 135. *Barrandia ultima* sp. nov., above. Lower Llandeilo, stream section 400 yd (365 m) NE of Gorse, SO 072617. Fig. 130, internal mould of meraspid ? of degree 6, BU 456 (*ex* Chamberlain Coll. 147/14), ×6. Fig. 131, Paratype. Internal mould of cranidium, showing axial furrows extending to lateral margins and relatively wide fixigena, It.2944, ×6. Fig. 132, internal mould of pygidium with parathoracic segment and furrowed axis, It.2947, ×6. Fig. 133, internal mould of meraspid of degree 5 or 6, It.2946, ×6. Fig. 135, Paratype. Internal mould of pygidium with parathoracic segment, It.2943, ×6.

Fig. 134. *Barrandia cordai* M'Coy, p. 156. Lower Llandeilo, stream section 15 yd (14 m) SW of the old quarry 350 yd (320 m) west of Maesgwynne, SO 059566. Internal mould of hypostoma, It.2948, ×4.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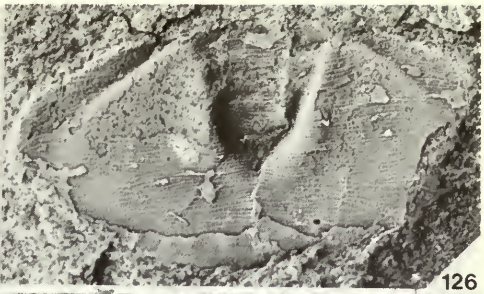
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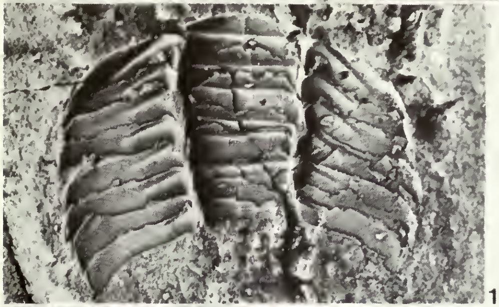
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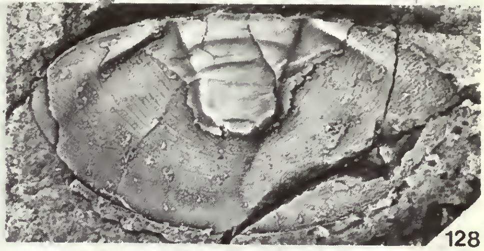
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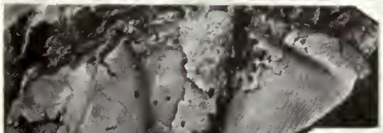
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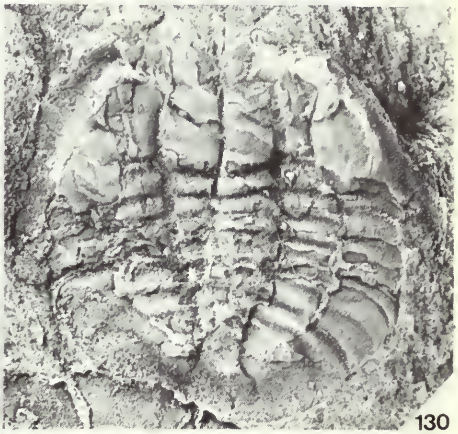
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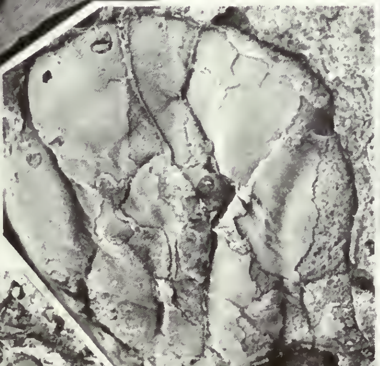
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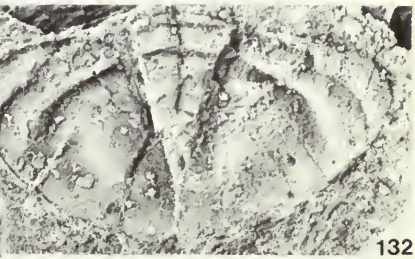
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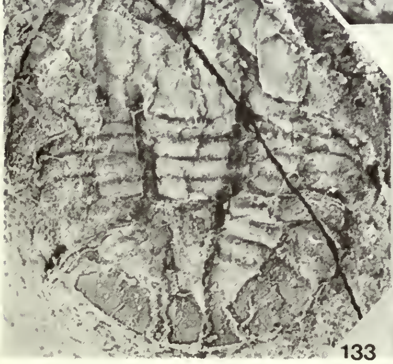
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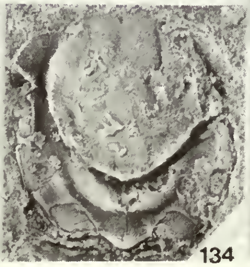
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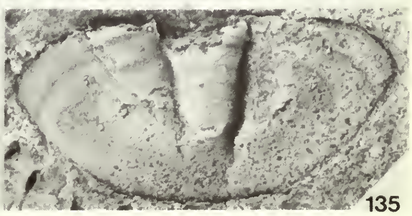
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Thorax appears to be identical to *B. cordai*.

Pygidium differs from *B. cordai* in that four axial rings and a short terminal piece are almost certainly present (Fig. 135) and the doublure is narrower. Paratype pygidium It.2943, with its parathoracic segment, is only a little smaller than other pygidia with no such segment and is another example of late retention of the eighth thoracic segment in the pygidium (p. 158).

Ontogeny. Two late meraspides are known, but determination of their precise degree is not possible. BU 456 is most likely a degree 6 and It.2946 may be degree 5 or 6.

Cephalon, as far as can be determined, very similar to that of holaspides. BU 456 shows the eye but no trace of lens structures. Genal spine (Fig. 130) possibly relatively larger than in holaspides but this may be due to distortion. BU 456 also shows parts of six thoracic segments, which appear to be freely articulating, and two parathoracic segments. It.2946 has the anterior region very poorly preserved and it is more difficult to assess where the front of the transitory pygidium lies. It is believed that there are also two parathoracic segments present. In outline it is similar to the holaspis pygidium, but it is relatively longer with a larger axis.

Discussion. This species is distinguished from other *Barrandia* species by the relatively narrow pygidial doublure. The species is the youngest known *Barrandia*, from beds near the top of the *Glyptograptus teretiusculus* Shales above the level at which *Ogyginus corndensis* dies out. Other species previously recorded from approximately this level or higher (Elles 1940) are here placed in *Homalopteon*.

Genus ***HOMALOPTEON*** Salter, 1866

Diagnosis. Exoskeleton oval, depressed and subisopygous. Glabella expanded frontally; four pairs of very shallow lateral glabellar furrows; axial furrow shallow particularly anteriorly; fixigena narrow expanding posteriorly. Eye well developed; librigenae fused; genal spine short. Eight thoracic segments, doublure extending under slightly less than half pleural width. Pygidium subsemicircular; axial rings prominent; up to three ribs on gently convex pleural field.

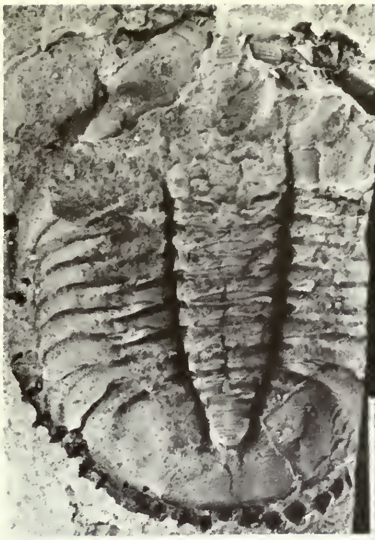
Type species. *Ogygia portlockii* Salter, 1849.

Distribution. The type species is from the Raheen Shales (Caradoc) of Co. Waterford, Ireland. In central Wales the genus is present in the uppermost lower, and middle to upper Llandeilo; it was also recorded by Salter (1867 : 179) from Abereiddy Bay, probably from beds of lower Llandeilo age.

Discussion. The genus was separated at subgeneric level from *Barrandia* by Salter (1866 : 137–138) on characters which are summarized below. He placed both in the Asaphidae, but Reed (1931 : 468), having given full generic status to *Homalopteon*, assigned them to the Nileidae on the basis of the absence of the median suture. In Moore (1959 : O352) Jaanusson tentatively placed *Homalopteon* back in the Asaphidae. *Homalopteon* is certainly very closely allied to *Barrandia* and is thus a nileid.

Figs 136, 140. *Barrandia ultima* sp. nov., p. 160. Lower Llandeilo, stream section 400 yd (365 m) NE of Gorse, SO 072617. Fig. 136, **Holotype.** Internal mould showing traces of hypostoma and cephalic doublure, It.2945, ×4. Fig. 140, Paratype. Internal mould of nearly complete specimen, BU 455 (*ex* Chamberlain Coll. 147/14), ×4.

Figs 137–139, 141–144. *Homalopteon radians* (M'Coy), p. 164. Figs 137–138, 141–142, Lower Llandeilo, small quarry at SW end of Pen-cerig Lake, SO 043541. Fig. 137, internal mould of cranidium showing traces of glabellar furrows, It.2960, ×5. Fig. 138, internal mould showing cephalic axial furrows, It.2950, ×5. Fig. 141, external mould of thorax and pygidium showing surface sculpture, It.2949, ×2. Fig. 142, internal mould of larger pygidium showing four axial rings and a terminal piece, It.2961, ×2. Figs 143–144, Lower Llandeilo, 'Pen-cerig, Builth'; probably from small quarry at SW end of Pen-cerig Lake, SO 043541. Fig. 143, Lectotype. Internal mould of pygidium, SM A16691, ×4. Fig. 144, Paralectotype. External mould of pygidium, SM A16692, ×4. Fig. 139, Lower Llandeilo, Builth, exact loc. unknown. Internal mould of complete specimen, NMW 98.433, ×2.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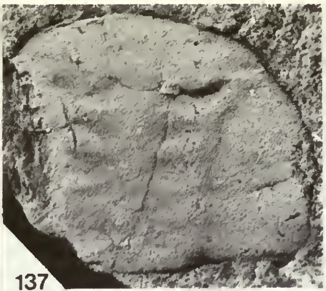
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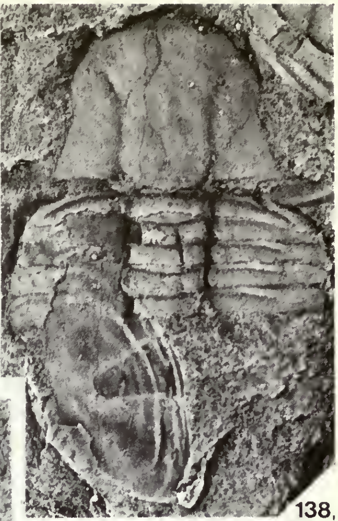
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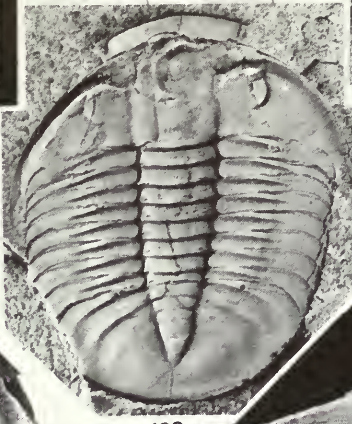
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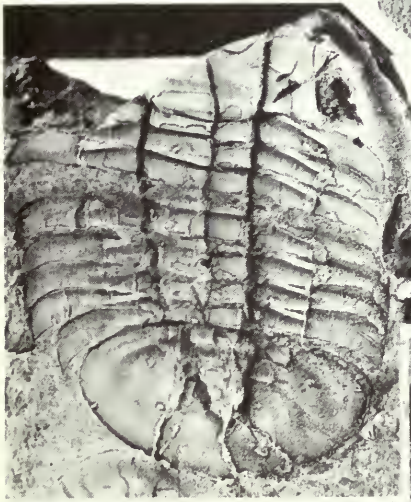
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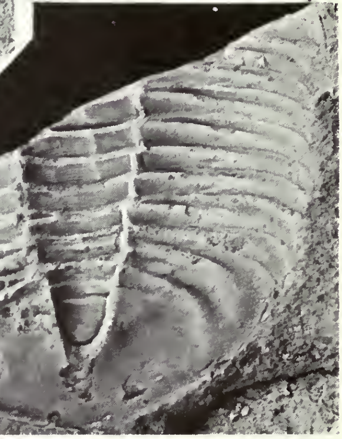
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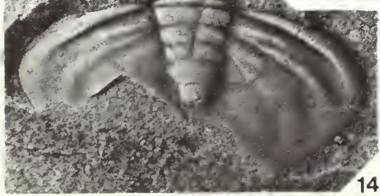
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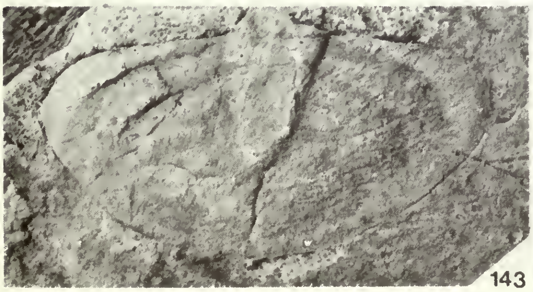
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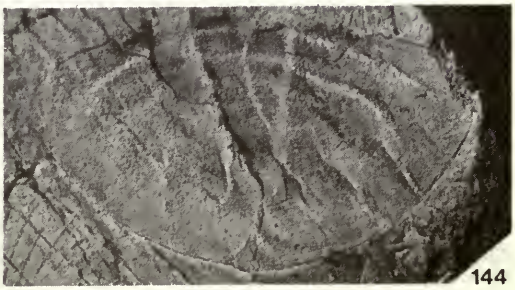
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In retaining *Homalopteon* as a separate genus, some modification to Salter's original definition is required (Table 17).

Table 17. Summary of important differences between *Barrandia* and *Homalopteon*, as envisaged by Salter (1866) and the present author.

	After Salter		Herein	
	Barrandia	*Homalopteon*	*Barrandia*	*Homalopteon*
Glabella	Unfurrowed	Furrowed	Unfurrowed	Four furrows
Axial furrow	Incomplete	Complete	—	—
Fixigena	—	—	Narrow posteriorly; no posterior border	Expanded posteriorly; narrow posterior border
Eye	Subcentral	Anterior	—	—
Pleura	Fulcrum near axis	Fulcrum remote	—	—
Doublure	—	—	>½ pleural width	<½ pleural width
Pygidial axis	Unfurrowed	Furrowed	Weakly furrowed; up to 4 axial rings	Strong furrows; up to 5 axial rings
Pleural field	Unfurrowed	Furrowed	Generally unfurrowed; occasionally with up to 2 weak furrows	Furrowed; up to 4 prominent ribs

Salter's use of the cephalic axial furrow as a diagnostic feature was unsatisfactory, as the anterior portion is very shallow in *Homalopteon* and is easily obliterated by poor preservation. Further, the position of the eye can no longer be regarded as diagnostic, for the 'eye' in the type specimen of *B. cordai* (the only specimen available to Salter) is merely a broken area of shale (p. 158); new material from Builth shows the eye to be more anteriorly positioned, as in other species of *Barrandia* from the Shelve region. Similarly the pygidial axis of *B. cordai*, and also other species of *Barrandia* (Whittard 1961*a* : 221–228), is now known to be weakly furrowed.

Homalopteon radians (M'Coy, 1849)
(Figs 137–139, 141–145, 147–148, 150–151, 153, 155–159)

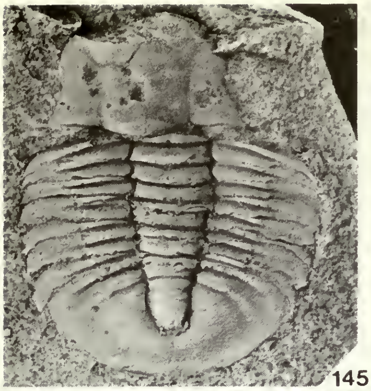
1849 *Ogygia radians* M'Coy : 408–9.
1866 *Barrandia* (*Homalopteon*) *radians* (M'Coy) Salter : 140.
1940 *Barrandia* (*Homalopteon*) *radians* (M'Coy); Elles (*pars*) : 410–412, 417, 432.
1961*a* *Barrandia radians* (M'Coy); Whittard : 227–228 (gives other earlier synonymy).

DIAGNOSIS. *Homalopteon* having generally three axial rings on pygidium with second pygidial rib only weakly developed.

TYPE MATERIAL. In his original description, M'Coy (1849 : 408) gave no figure, nor any indication of the specimens upon which his description was based. However, specimens SM A16691

Figs 145, 147–148, 150–151, 153, 155–156. *Homalopteon radians* (M'Coy), above. Lower Llandeilo, small quarry at SW end of Pen-cerig Lake, SO 043541. Fig. 145, internal mould of nearly complete specimen, showing thoracic doublure, It.2954, ×2. Fig. 147, external mould of early meraspis, It.2957, ×7·5. Fig. 148, internal mould of meraspid ? of degree 5, showing traces of parathoracic segments in the transitory pygidium, It.2956, ×5. Fig. 150, internal mould of meraspid of degree 7, showing traces of eyes and hypostoma, It.2952, ×5. Fig. 151, internal mould of hypostoma with attached librigena, It.2953, ×6. Fig. 153, external mould of young holaspid pygidium, It.2959, ×7·5. Fig. 155, internal mould of meraspid of degree 6, showing two parathoracic segments in the transitory pygidium, It.2955, ×5. Fig. 156, internal mould of meraspid ? of degree 6, It.2958, ×5.

Figs 146, 149, 152, 154. *Homalopteon murchisoni* sp. nov., p. 168. Middle-upper Llandeilo, quarry at Gwern-yfed-fâch, ½ ml (805 m) SE of Builth Road station, SO 030526. Paratype. Internal and external moulds of left librigena showing eye region and sculpture of cephalic doublure, It.2963. Figs 146, 152, ×5; Figs 149, 154, ×12.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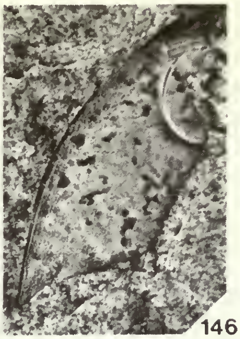
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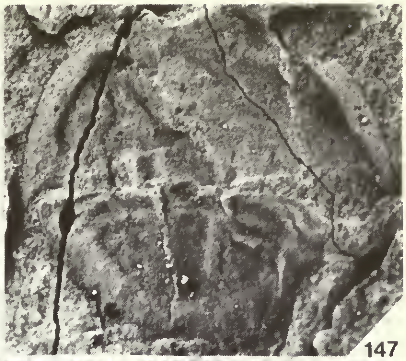
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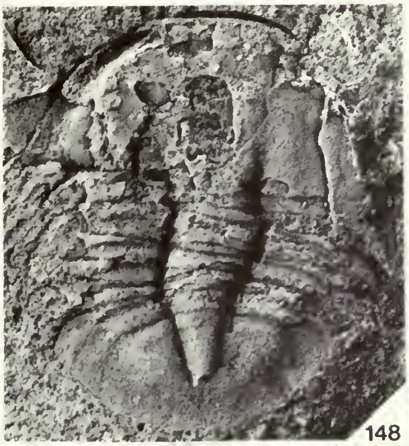
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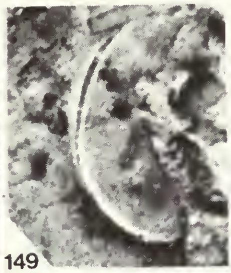
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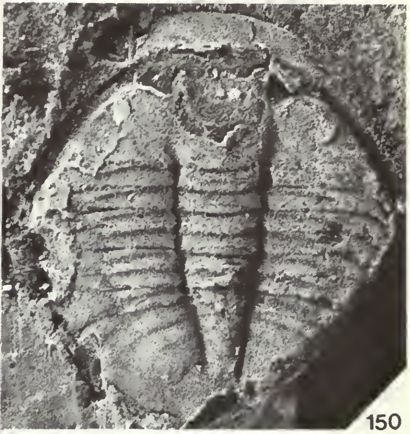
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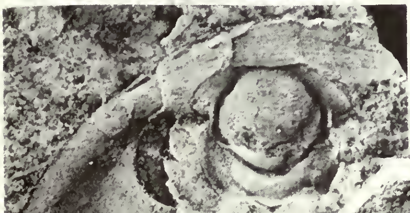
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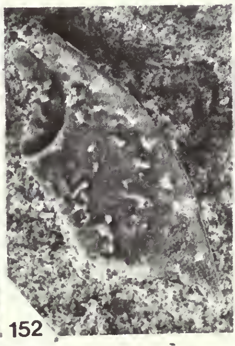
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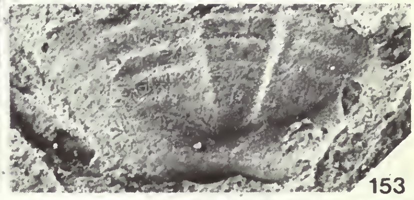
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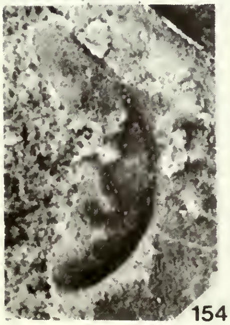
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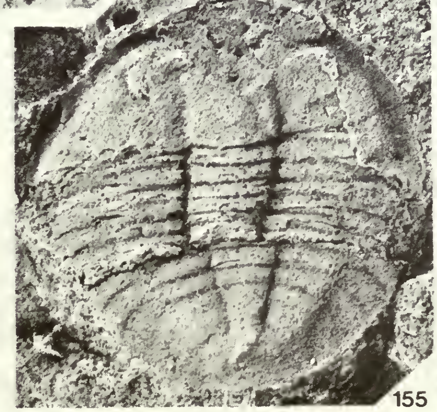
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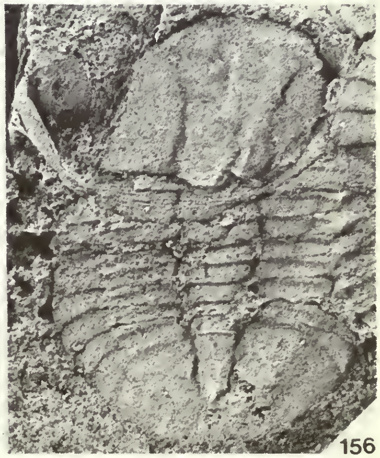
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(figured Sedgwick & M'Coy 1851 : pl. 1F, fig. 2) and SM A16692 are the only specimens known from M'Coy's original collection in the Sedgwick Museum and are here taken as syntypes. Whittard (1961*a* : 227) referred to A16691 as holotype and A16692 as paratype; this is tantamount to selecting them as lectotype and paralectotype, respectively, and they should be designated as such. The lectotype (Fig. 143) is an internal mould of a pygidium; the paralectotype (Fig. 144) an external mould of a pygidium.

DIMENSIONS (in mm).

	W	Y	Z
SM A16691	15·0	4·5	7·4
SM A16692	14·5	–	8·0

For explanation of symbols see Fig. 1.

LOCALITY AND HORIZON. Both type specimens are recorded as from Pen-cerig, near Builth, and are thought to be from the small quarry at the south-western end of Pen-cerig Lake, from near the top of the *Glyptograptus teretiusculus* Shales.

DISTRIBUTION. The species is most common in the uppermost lower Llandeilo of the Builth region. It may also be present as an extreme rarity in the Shelve region in beds of lower Llanvirn age, but the exact systematic position of the specimen described by Whittard (1961*a* : 227–228) as *Barrandia* cf. *radians* is not certain.

DESCRIPTION. Complete individuals slightly over one and a quarter times as long as wide (Fig. 139).

Cephalon semielliptical, slightly over twice as wide as long and almost exactly one-third of total exoskeletal length. Glabella occupies about one-quarter of cephalic width posteriorly, and is more or less parallel-sided over posterior two-thirds of its length. Glabella expands quite sharply anteriorly to occupy entire cephalic width, the axial furrow being deflected to cut the lateral margin (Fig. 145); preglabellar field and anterior border absent. Glabella with four pairs of evenly-spaced, weakly-developed glabellar furrows (Fig. 137). Anterior pair situated opposite maximum glabellar width; posterior about one-third of glabellar length from posterior margin. The furrows are more or less transversely directed but adaxially deflected slightly to posterior. Anterior pair slightly the longest, though all fail to reach the axial furrow and axially leave the mesial quarter of the glabella smooth. A further very weak pair of short, transversely-directed furrows with a small median node occasionally present between their axial extremities is developed about mid-way between the posterior pair of glabellar furrows and the posterior margin. These represent the occipital furrows, and the weakly-developed, forwardly-convex furrow situated behind them, a posterior band furrow. Axial furrow extends with very little shallowing to lateral cranidial margin. In some specimens the furrow appears to die out anteriorly owing to imperfect preservation. Posterior branch of facial suture extends from slightly under half-way along the posterior margin from the axial furrow and is straight and directed slightly axially until it reaches the eye. In front of the eye the suture is gently convex laterally, becoming coincident with the axial furrow anteriorly. Fixigena virtually flat and smooth. Librigenae fused (Fig. 151), smooth and gently convex, sloping down laterally to a slightly concave border region. Short genal spine extends to second thoracic segment. As in *Barrandia*, eye lacks any preserved lens structures (Fig. 139).

Cephalic doublure convex dorsally with fine terrace lines on both ventral and dorsal surfaces (Figs 151, 159). Anteriorly, doublure widens to form a projection abutting anterior wing of hypostoma. Hypostoma subrectangular, with small anterior wing extending for about one-third of hypostomal length. Lateral margin slightly convex outwards with very small posterior wing. Posterior margin with small median lip (Figs 151, 159). Anterior lobe circular and delimited by a well-developed furrow. Posterior lobe crescentic, short (*sag.*); maculae absent. Both ventral and dorsal surfaces bear fine terrace lines.

Thorax subrectangular. Axis occupies just under one-quarter of thoracic width anteriorly, tapers slightly (Fig. 139). Axial rings simple and defined by a well-developed axial furrow which tends to be slightly zetoidal, owing to the asymmetrical location of the swollen axial end of the posterior pleural band (Fig. 139). Pleurae falcate; each has a strong pleural furrow, axially lying nearly parallel to anterior margin, becoming deeper and deflected to be posterolaterally-directed at a point about one-third, finally dying out slightly over two-thirds, the way across the pleura (Fig. 139). Width of thoracic doublure slightly less than half pleural width (Fig. 145).

Pygidium generally a little over twice as wide as long. Anterior margin gently convex anteriorly; anterolateral corners obtusely rounded. Axis occupies just under one-quarter of pygidial width anteriorly, tapers posteriorly and extends for about three-fifths of pygidial length; terminates in an obtusely rounded terminal piece. Generally three, less commonly two or four axial rings developed (Figs 142, 157, 158). Pleural field very gently convex with no distinct border. Anterior border furrow prominent. One well-developed rib present with a shallow pleural furrow axially (Fig. 158). A second rib also present, but very weakly developed and commonly obscured by imperfections in preservation. In small holaspid specimens only the anterior rib appears to be developed, but inadequate data preclude any tests of correlation between size and presence of a second rib. Ventral doublure slightly narrower than that of *Barrandia*, and underlies approximately the outer two-thirds of the pleural field, becoming a little narrower posteromedially. Dorsal surface bears fine raised lines directed transversely, but slightly concave anteriorly (Fig. 141).

Ontogeny. A single specimen is known (Fig. 147) of a very early meraspis, probably of no higher degree than 2. It is more or less circular with length (*sag.*) of 5·2 mm. Cephalon shows no details apart from a well-developed doublure. Pygidial axis clearly defined but no details of axial rings preserved. As in later meraspides the pygidial region has a well-developed, slightly concave, border region.

The other four known meraspides are of degree 5 or above and, except for the transitory pygidial regions, they are very like the holaspid form. The cephalon is not well preserved in any of these, although It.2958 (Fig. 156) shows the axial furrow clearly developed and diverging anteriorly. It.2956, possibly a degree 5 meraspis, shows traces of two parathoracic segments, as does It.2955 (Fig. 155), a meraspis of degree 6. In the latter it is possible that these two segments may have been freely articulating. In the degree 7 meraspis (Fig. 150) only one parathoracic segment appears to be developed. In It.2958 it is not clear how many segments are present in the thorax, and although it seems most likely that seven are developed there are also indications of two parathoracic segments.

A small isolated pygidium in which three axial rings are developed (Fig. 153) is larger than a degree 7 transitory pygidium and may represent a young holaspis.

Table 18. Bivariate statistics for *Homalopteon radians* (M'Coy) from the small quarry at the south-western end of Pen-cerig Lake. All measurements in mm. For explanation of symbols see Fig. 1.

x : y	$\bar{x}$	var. x	$\bar{y}$	var. y	r	r_c	α	var. α	a	var. a	n
A : C_3	8·15	7·43	4·24	1·61	0·99	0·99	0·90	0·0027	0·47	0·0008	8
A : K_1	7·39	5·43	4·48	2·89	0·99	0·99	1·19	0·0021	–	–	17
W : Z	11·11	16·15	5·44	4·81	0·97	0·98	1·11	0·0021	–	–	29
W : X	11·49	20·98	2·66	1·42	0·98	0·99	1·11	0·0012	–	–	30
Y : X	3·36	1·66	2·66	1·20	0·96	0·96	1·07	0·0022	0·85	0·0015	38
Z : Y	5·42	4·14	3·21	1·23	0·98	0·98	0·93	0·0008	–	–	36

Table 19. Frequency distribution and mean and variance of axial rings on pygidia of *Homalopteon radians* (M'Coy) from the small quarry at the south-western end of Pen-cerig Lake. The suffix 'i' indicates the development of a further incipient ring, and such rings have been counted as half a ring in the calculation of the mean.

Number of axial rings	2	2i	3	3i	4
Number of specimens	4	1	15	1	2

mean = 2·9; var. = 0·29; n = 23.

Discussion. Although Reed (1931 : 468) considered the species to belong to *Barrandia* on the basis of the development of the cephalic axial furrow, the wide posterior part of the fixigena and the pygidial axial rings indicate its affinities with *Homalopteon*.

H. radians is similar to *H. murchisoni* sp. nov. (below) but is distinguished by its fewer pygidial axial rings and weaker furrowing of the pleural field. The type species, *H. portlockii*, may be distinguished by its greater posterior expansion of the fixigena and also its higher number of pygidial axial rings and pleural ribs.

Homalopteon murchisoni sp. nov.

(Figs 146, 149, 152, 154, 160–172)

1866 *Barrandia* (*Homalopteon*) *radians* (M'Coy); Salter (*pars*) : 140–142; pl. 19, fig. 4.
1940 *Barrandia* (*Homalopteon*) *radians* (M'Coy); Elles (*pars*) : 416–418, 421, 432.

Diagnosis. *Homalopteon* with three to five, typically four, axial rings visible on dorsal surface and two well-developed ribs on the pygidium.

Name. After R. I. Murchison.

Type material. Holotype: BU 457 (*ex* Chamberlain Collection 54/4) (Figs 161–2), internal and external moulds of large pygidium. Paratypes: It.2963 (Figs 146, 149, 152, 154), internal and external moulds of left librigena; It.2964 (Figs 167–8), internal mould of right librigena; It.2965 (Fig. 171), external mould of isolated hypostoma; It.2966 (Fig. 165), external mould of cranidium; It.2967 (Fig. 160), internal mould of pygidium; It.2968 (*ex* Straw Collection, Manchester University) (Fig. 164), internal and external moulds of pygidium and part of thorax; It.2969 (Fig. 169), internal and external moulds of hypostoma and librigenae; It.2970 (Fig. 166), internal and external moulds of pygidium; It.2971 (Fig. 163), internal and external moulds of cranidium; It.2972 (Fig. 172), internal mould of complete meraspis; It.2973 (Fig. 170), internal mould of hypostoma.

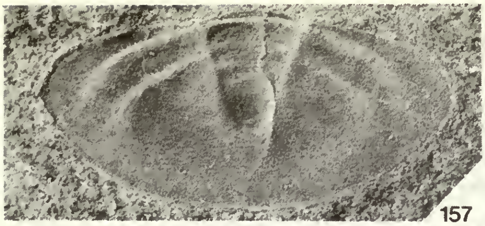
Dimensions (in mm).	A	J	J_1	J_2	K	T.L.
It.2966	4·4	*c.* 5·0	–	–	2·5	–
It.2971	12·3	17·0	10·9	13·4	7·3	–
It.2972	–	–	–	–	–	8·7

	W	X	Y	Z	H_1	H_5	H_7	H_8
BU 457	*c.* 28·8	6·7	10·5	11·3	–	–	–	–
It.2967	8·3	1·7	2·9	4·1	–	–	–	–
It.2972	6·0	–	–	–	–	–	–	–
It.2968	16·5	3·8	5·2	9·1	–	–	–	–
It.2965	–	–	–	–	7·0	6·6	6·7	5·5
It.2969	–	–	–	–	*c.* 6·3	–	*c.* 5·3	*c.* 4·2

For explanation of symbols see Fig. 1.

Figs 157–159. *Homalopteon radians* (M'Coy), p. 164. Lower Llandeilo, small quarry at SW end of Pencerig Lake, SO 043541. Figs 157, 158, internal and external moulds of pygidium, showing three axial rings, It.2962, ×5. Fig. 159, external mould showing ventral cephalic exoskeleton with no median suture, It.2951, ×3.

Figs 160–166. *Homalopteon murchisoni* sp. nov., above. Figs 160–162, 165, Middle-upper Llandeilo, quarry at Gwern-yfed-fâch, $\frac{1}{2}$ ml (805 m) SE of Builth Road station, SO 030526. Fig. 160, Paratype. Internal mould of small pygidium with relatively long axis and traces of three pairs of ribs, It.2967, ×6. Figs 161–162, **Holotype.** Internal and external moulds of damaged pygidium, showing five axial rings and terminal piece, BU 457 (*ex* Chamberlain Coll. 54/4), ×2. Fig. 165, Paratype. External mould of cranidium showing glabellar furrows, It.2966, ×6. Figs 163, 166, Middle-upper Llandeilo, middle quarry, Llanfawr, Llandrindod, SO 066617. Fig. 163, Paratype. Internal mould of cranidium, showing traces of posterior band on occipital ring and posterior border furrows, It.2971, ×3. Fig. 166, Paratype. Internal mould of pygidium with only three, possibly four, axial rings, It.2970, ×5. Fig. 164, Middle-upper Llandeilo, ? middle quarry, Llanfawr, Llandrindod, SO 066617. Paratype. Internal mould of thorax and pygidium, It.2968 (*ex* Straw Coll., Manchester University), ×2.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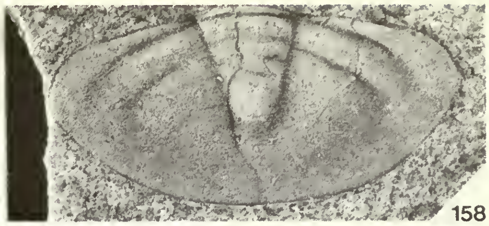
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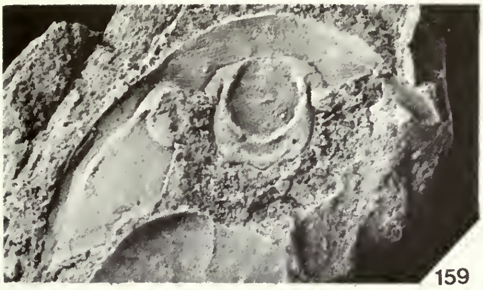
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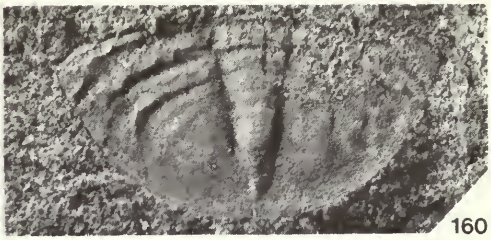
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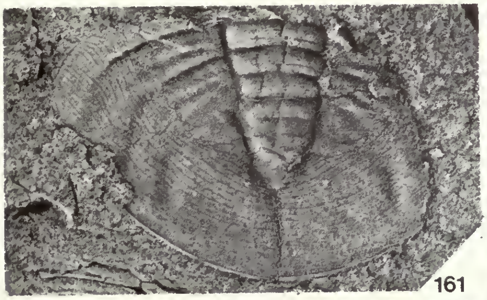
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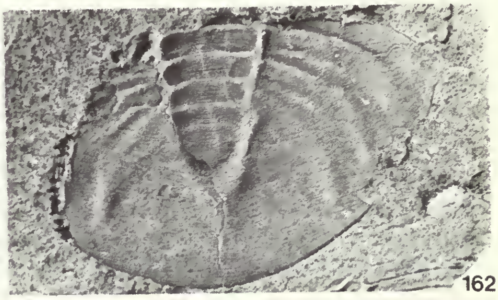
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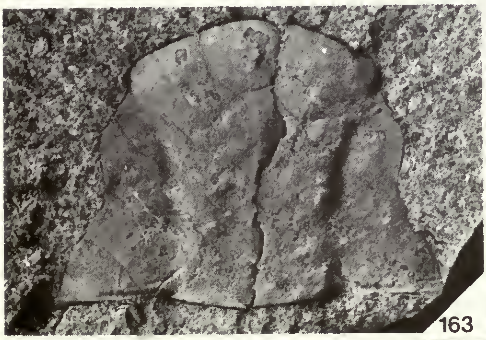
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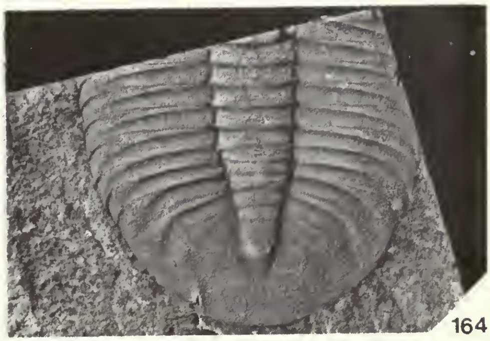
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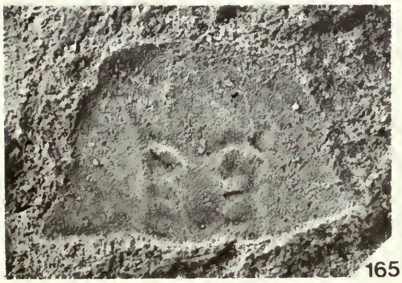
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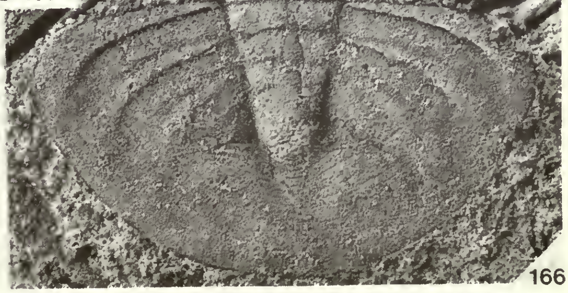
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Locality and horizon. The holotype and paratypes It.2963–7 are from the quarry at Gwern-yfed-fâch, half a mile (805 m) south-east of Builth Road station. The other paratypes are from the middle quarry, Llanfawr, Llandrindod. Both localities are in the *Nemagraptus gracilis* Shales. The species is known only from the two localities yielding the type material.

Description. The species is similar to *H. radians* and only a comparative description is given.

Cephalon similar to *H. radians* although there may be slight differences in glabellar furrowing (compare Fig. 137 with Figs 163, 165). Posterior border is developed on fixigena, separated by a narrow, though clearly-developed, border furrow (Fig. 163). Eye devoid of visible lenses (Figs 146, 149, 152, 154, 167–8).

Hypostoma (Figs 171–2) and only known thorax (Fig. 164) similar to *H. radians.*

Pygidium typically with four axial rings and two well-developed ribs; occasionally there is an indication of a third rib (Fig. 160).

Ontogeny. One poorly-preserved specimen is thought to be a meraspis of degree 3 or 4 (Fig. 172). As far as can be determined its exoskeleton, including the hypostoma, is very like that of holaspides except for the number of thoracic segments.

Biometrical data. Very few data concerning the cephalon are known from the holotype locality, so details are given based on material from the middle quarry, Llanfawr (Table 20) from which much of the paratype material was recovered. Pygidial data from both type localities are given.

Table 20. Bivariate statistics of *Homalopteon murchisoni* sp. nov. Upper part of table from the middle quarry, Llanfawr; lower part from the quarry at Gwern-yfed-fâch. All measurements in mm. For explanation of symbols see Fig. 1.

x : y	$\bar{x}$	var. x	$\bar{y}$	var. y	r	r_e	α	var. α	a	var. a	n
A : C_3	9·47	4·51	5·05	1·09	0·99	0·99	0·92	0·0059	0·49	0·0017	6
A : J_1	10·06	2·99	8·98	1·69	0·98	0·98	0·84	0·0071	0·75	0·0060	5
A : J_2	10·22	3·81	11·15	3·43	0·99	0·99	0·87	0·0038	0·95	0·0045	4
A : K_1	9·47	4·51	5·47	1·80	1·00	1·00	1·09	0·0024	0·63	0·0008	6
W : Z	13·79	13·91	7·61	5·56	0·99	0·99	1·14	0·0052	0·63	0·0017	8
W : X	13·90	12·28	3·22	0·86	0·98	0·99	1·13	0·0051	0·26	0·0003	9
Y : X	5·26	2·61	3·69	1·24	0·93	0·93	0·98	0·0103	0·69	0·0053	14
Z : Y	9·31	9·06	5·41	2·68	0·95	0·95	0·94	0·0067	0·54	0·0023	14
W : Z	9·23	9·95	4·83	4·85	0·98	0·99	1·31	0·0058	–	–	9
W : X	9·64	9·69	2·21	0·74	1·00	1·00	1·19	0·0009	–	–	8
Y : X	3·13	1·22	2·30	0·62	0·99	0·99	0·97	0·0030	0·71	0·0017	10
Z : Y	6·73	16·31	4·12	6·40	0·99	0·99	1·02	0·0012	0·63	0·0005	12

Table 21. Frequency distribution and mean and variance of axial rings on pygidia of *Homalopteon murchisoni* sp. nov. Upper part of table from quarry at Gwern-yfed-fâch; lower part from the middle quarry, Llanfawr. The suffix 'i' indicates the development of a further incipient ring, and such rings have been counted as half a ring in the calculation of the means.

Number of axial rings	3	3i	4	4i	5
Number of specimens	3	0	5	1	1
mean = 3.85; var. = 0·45; n = 10					
Number of specimens	7	0	7	0	0
mean = 3·50; var. = 0·27; n = 14					

Comparison of these and the equivalent data for *H. radians* (both data sets include internal and external moulds) shows that the mean number of axial rings developed in *H. murchisoni* is significantly higher than in *H. radians.* While in *H. murchisoni* the mean is higher in the sample from Gwern-yfed-fâch, the difference between this and that of the Llanfawr sample is not significant. Contingency tests show that the difference between the axial ring counts of the two species is not because of any correlation between pygidial size and number of rings.

DISCUSSION. The species is obviously closely related to *H. radians*, but the greater development of the pygidial furrowing together with the small cephalic differences warrant its specific separation. Morphologically the species provides a link between *H. radians* and *H. portlockii*, the pygidial furrowing being even more marked in the type species.

Family **ODONTOPLEURIDAE** Burmeister, 1843
Subfamily **ODONTOPLEURINAE** Burmeister, 1843

Genus ***DIACANTHASPIS*** Whittington, 1941

DIAGNOSIS. Whittington's emendment (1956 : 210) of his original diagnosis (1941 : 501) is extended to cover species with up to eight pairs of horizontally-directed pygidial border spines.

TYPE SPECIES. *Diacanthaspis cooperi* Whittington, 1941.

DISTRIBUTION. Accepting the tentative generic assignment of the Builth specimen, the genus ranges in Britain from uppermost lower Llanvirn (*D. bifidus* Zone) to Ashgill (Zones 1–3) (Tripp 1954, Whittington 1968, Price 1974) and possibly into the lower Llandovery (Temple 1969). It is also recorded from the Caradoc of Estonia (Bruton 1968), Norway (Bruton 1965) and eastern United States of America (Whittington 1956); the Ashgill of Ireland (Dean 1974), Bornholm (Poulsen 1966), Sweden (Bruton 1966) and Poland (Kielan 1960). In addition it is possibly present in the Arenig (Zones H-L) of the western United States of America (Hintze 1953, Ross 1967, 1970, Young 1973).

DISCUSSION. The earliest certain occurrence of the genus is in the basal Caradoc (lower Edinburgh Limestone) of North America, the first unquestioned occurrence in Britain being from the mudstones in Craighead Quarry, near Girvan, from a horizon probably a little higher in the Caradoc (Tripp 1954 : 688). The possible appearance of the genus in the lower Llanvirn at Builth is of particular interest. It is one of the few possible pre-Llandeilo records of odontopleurids. With the provisional placing by Whittington & Bohlin (1958 : 41–42) of *Ceratocephala solis* ? (Öpik) (Bohlin 1949 : 539, 560, 566, fig. 8) and '*Acidaspis*' *solis* Öpik, 1925 in the apianurine genus *Boedaspis* Whittington & Bohlin, 1958, the only records of earlier odontopleurinids are restricted to *Diacanthaspis* ? *trispineus* Young, 1973, from the Arenig of the western United States of America, and a probable cranidium of *Diacanthaspis* sp. (Hintze 1953 : pl. 19, figs 16, 16a; Ross 1970 : 10) and other specimens of *Diacanthaspis* (Ross 1967 : 30; 1970 : 46), together with possible odontopleurinid fragments, from the early Arenig of Västergötland (Tjernvik 1956 : 264). The latter have been shown by Bruton (1966) to belong to *Periallaspis*, a genus of unknown subfamilial affinities.

Diacanthaspis ? sp. A
(Fig. 176)

FIGURED SPECIMEN. It.3020, internal mould with eight thoracic segments attached to pygidium. Dimensions (in mm): anterior thoracic width – 3·7; anterior thoracic axial width – 1·1; posterior thoracic axial width – 0·8; thoracic length – 2·0; anterior pygidial width – *c.* 2·1; anterior pygidial axial width – 0·7; pygidial length – 0·6; pygidial border spine length – 0·3.

LOCALITY AND HORIZON. The single specimen is from the uppermost *Didymograptus bifidus* Shales exposed in the cliff section on the left bank of the Howey Brook, half a mile (805 m) ESE of Carregwiber.

DESCRIPTION. Cephalon unknown. Thorax apparently subrectangular; of at least eight segments with four or five major spines on posterior band. Axis convex and occupying about one-quarter of total width anteriorly, tapering slightly to the rear; articulating furrow broad and bowed forwards mesially. Axial furrow deep with apodemes at anterior of each segment. Pleural furrow shallow, more or less transversely-directed, separating anterior and posterior bands of approximately equal width (*exsag.*). Anterior band flat with short pleural spine. Posterior band convex (*exsag.*) with four or five spines along its crest, outer two or three being more closely spaced than inner ones; distally the band is prolonged into a long pleural spine which becomes progressively longer and more backwardly-curved on successive segments.

Pygidium with more than six, possibly eight pairs of horizontally-directed pygidial border spines; upwardly-directed (?) spine opposite base of sixth border spine; smaller spines opposite second and fourth spines. Excluding the spines, it is triangular, about three times as wide as long. Axis occupies about one-third of anterior width and tapers gently to posterior. As in thorax no trace of any spines is seen on the axis. Pleural field unfurrowed, but a pleural ridge is developed opposite the first axial ring, initially transversely-directed, but turning abruptly posteriorly and ending in a large spine base (spine is not preserved but presumably was directed upwards) at the base of sixth border spine. Two further smaller spine bases occur opposite the second and fourth border spines.

Discussion. The generic placing of odontopleurids is difficult when cephalic details are lacking and the affinities of the Builth specimen are not certain. It is clearly not closely related to *Periallaspis* (Bruton 1966 : 29; pl. 6, figs 4–6; text-figs 7A, B), and it is best compared to either *Primaspis* R. & E. Richter, 1917 or *Diacanthaspis* Whittington, 1941, both Ordovician odontopleurine genera. However, early examples of *Primaspis*, for example *P. multispinosa* (Bruton 1965 : pl. 2, fig. 3), *P.* cf. *whitei* (Whittard 1961*a* : pl. 27, fig. 8), *P.* cf. *simulatrix* (Whittard 1961*a* : pl. 27, fig. 10) and *P.* ? sp. (MacGregor 1963 : pl. 116, fig. 22), may all be distinguished by their broadly curved pleural ridge. Similarly, this specimen may be distinguished from all known *Diacanthaspis* by the presence of the major upwardly-directed spine opposite the second and fourth border spines. If it should subsequently be shown that eight border spines are indeed developed then this also would distinguish it from all others except *D. sladensis* (see Temple 1969). D. L. Bruton (personal communication) has pointed out that the position and granulation of the pygidial pleural ridge is very like that found in *Odontopleura*, a genus currently restricted to two or three European Silurian species. The granulation on the thoracic pleurae, however, shows a close similarity to that of many *Diacanthaspis* and on balance it is believed the present specimen shows closest affinity to that genus.

Odontopleuridid gen. et sp. indet.
(Figs 174–175)

Figured specimen. It.3021, internal and external moulds of librigenal fragment.

Locality and horizon. Stream section 400 yd (365 m) north-east of Gorse, Llandrindod, in *Glyptograptus teretiusculus* Shales.

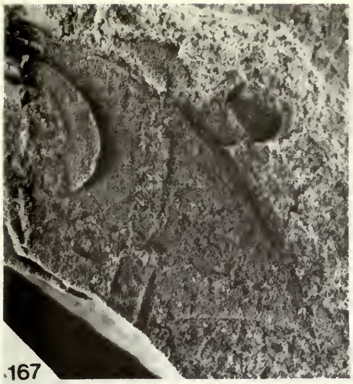
Figs 167–172. *Homalopteon murchisoni* sp. nov., p. 168. Figs 167–168, 171, Middle-upper Llandeilo, quarry at Gwern-yfed-fâch, ½ ml (805 m) SE of Builth Road station, SO 030526. Figs 167–168, Paratype. Internal mould of right librigena, It.2964. Fig. 167, ×4; Fig. 168, ×10. Fig. 171, Paratype. External mould of hypostoma, It.2965, ×4. Figs 169–170, 172, Middle-upper Llandeilo, middle quarry, Llanfawr, Llandrindod, SO 066617. Fig. 169, Paratype. External mould of hypostoma with attached librigenae, showing lack of median suture and relative position of the hypostoma, It.2969, ×4. Fig. 170, internal mould of hypostoma, It.2973, ×4. Fig. 172, internal mould of meraspid of degree 3 or 4, It.2972, ×5.

Fig. 173. *Rorringtonia* sp., p. 174. Middle-upper Llandeilo, quarry at Gwern-yfed-fâch, ½ ml (805 m) SE of Builth Road station, SO 030526. Internal mould of cranidium, It.3022, ×7·5.

Figs 174, 175. Odontopleuridid gen. et sp. indet., above. Lower Llandeilo, stream section 400 yd (365 m) NE of Gorse, SO 072617. External and internal moulds of librigenal fragment, It.3021, ×8.

Fig. 176. *Diacanthaspis* ? sp. A, p. 171. Lower Llanvirn, cliff section on left bank of Howey Brook, ½ ml (805 m) ESE of Carregwiber, SO 089582. Internal mould of pygidium and part of thorax, It.3020, ×10.

Fig. 177. *Ogyginus* cf. *intermedius* Elles, p. 137. Lower Llanvirn, left bank of upper reaches of Camnant Brook, 270 yd (247 m) S 13° W of the fence crossing near the stream source, SO 088575. Internal mould of pygidium, It.2890, ×1.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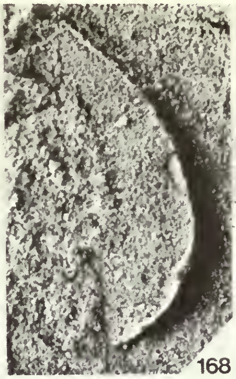
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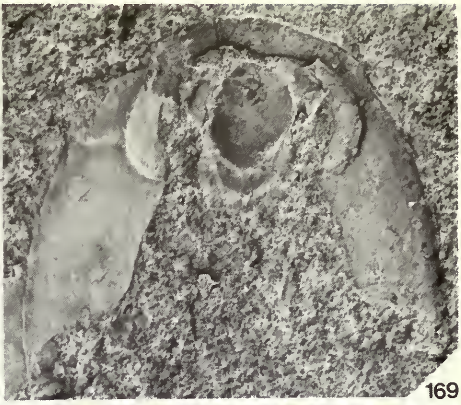
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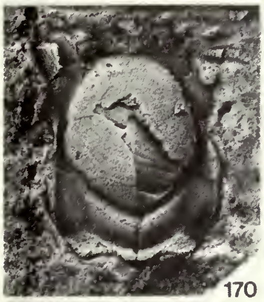
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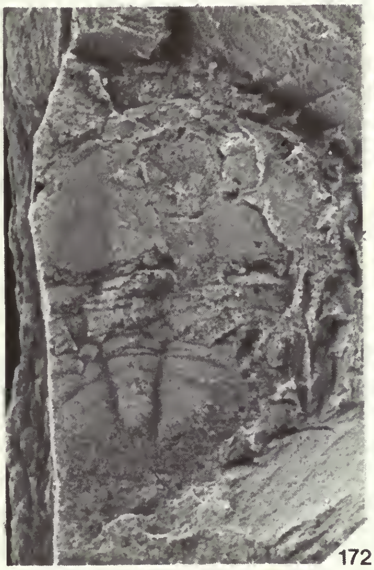
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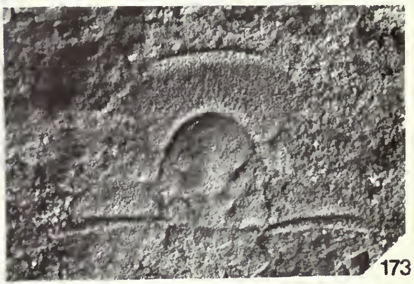
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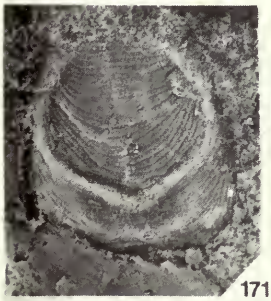
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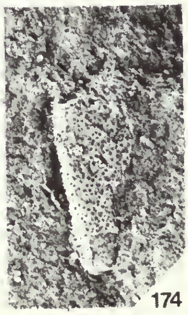
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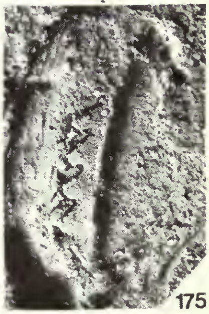
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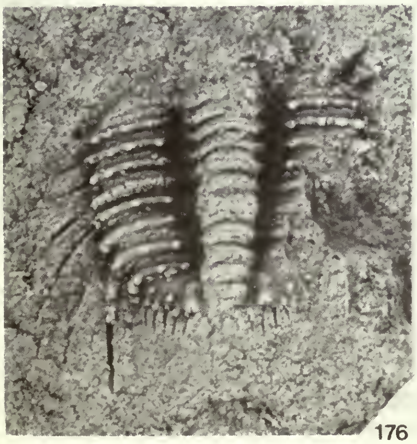
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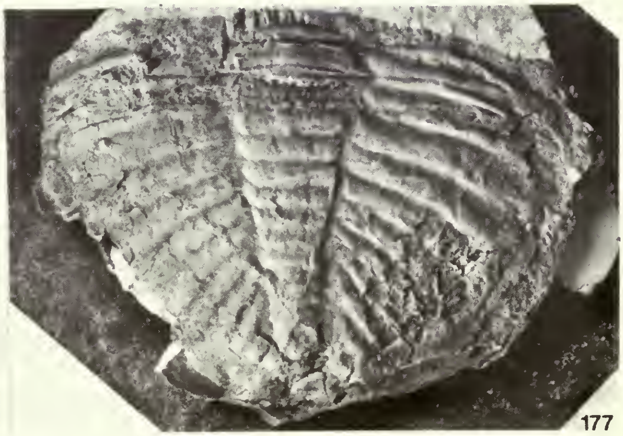
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DESCRIPTION. The single librigenal fragment shows a well-developed border region and bases of four stout lateral cephalic border spines. External surface bears irregularly-spaced granules about 0·3 mm in diameter.

DISCUSSION. This specimen is the only odontopleuridid so far recorded from the Llandeilo of the Builth region. It is similar to librigenae attributed to *Primaspis whitei* (Whittard 1961*a*: pl. 27, fig. 7) from beds of similar age at Shelve, but differs in having a sharper border ridge.

Family **PROETIDAE** Salter, 1864

Genus ***RORRINGTONIA*** Whittard, 1966

DIAGNOSIS. See Owens (1973 : 76).

TYPE SPECIES. *Rorringtonia flabelliforme* Whittard, 1966.

DISTRIBUTION. The genus is known from the Rorrington Beds (Caradoc) of the Shelve region, the *Nemagraptus gracilis* Shales (middle to upper Llandeilo) of the Builth region, the Balclatchie Group (Caradoc) near Girvan and from the Glenkiln Shales near Moffat (J. K. Ingham, personal communication 1975).

DISCUSSION. Whittard regarded the familial affinities of this genus as uncertain. The author concluded (1967, unpublished thesis) that it was most likely an early proetid, a conclusion supported by more recent work on the Proetidae by Owens (1973) and Fortey & Owens (1975). As noted by Owens, *Rorringtonia* exhibits many similarities to *Pseudoproetus* Poulsen, 1934, and may indeed be a junior synonym of Poulsen's genus.

Rorringtonia sp.

(Fig. 173)

1973 *Rorringtonia* sp. 1 Owens : 78.

FIGURED SPECIMEN. It. 3022, internal and external moulds of cranidium. Dimensions (in mm): cranidial length – 3·5; glabellar length excluding occipital ring – 2·1; glabellar length including occipital ring – 2·3; length (*sag.*) of frontal area – 1·2; length (*sag.*) of preglabellar field – 1·0; maximum cranidial width – 9·0; anterior cranidial width – *c.* 3·0; distance between posterior of palpebral lobes – 2·7; maximum glabellar width – 2·0.

LOCALITY AND HORIZON. Quarry at Gwern-yfed-fâch, half a mile (805 m) south-east of Builth Road station; *Nemagraptus gracilis* Shales.

DESCRIPTION. The single cranidium is small and gently convex. Glabella parabolic in outline, about two-thirds length of cephalon, and, excluding occipital ring, slightly longer than wide. Three pairs of lateral glabellar furrows developed; anterior pair very weak; median and posterior pairs, though possibly a little distorted, strong and directed inwards and backwards at about 45°. Posterior pair shallow mesially and deflected posteriorly, just failing to reach the occipital furrow. Median pair uniformly deep and extending about half-way to the mid-line on each side. In lateral view, convexity of glabella greatest anteriorly, sloping gently down to rear; maximum elevation between anterior lateral glabellar furrows. Glabella bounded by deep, narrow axial furrow. Preglabellar field long and only gently convex, bounded anteriorly by wide, shallow, gently curved anterior border furrow. Occipital ring poorly preserved; occipital furrow moderately deep and nearly straight; small occipital node may be present.

Eye probably developed, situated near axial furrow and opposite median lateral glabellar furrow. Course of facial suture uncertain, but anterior branch moderately divergent forwards; posterior branch directed transversely from posterior of palpebral lobe, curving gently to cut posterior margin. Posterior border furrow deep and more or less straight, separating a narrow (*sag.*) border which widens laterally. External surface of the cranidium appears to be smooth.

DISCUSSION. This specimen closely resembles *R. flabelliforme* Whittard, 1966 from the basal Caradoc Series of the Shelve region, but appears to differ in that the glabella, excluding the occipital ring, is slightly longer than wide. Further, the occipital furrow in the Builth specimen is not bowed forwards and the posterior lateral glabellar furrow shows no branching at its inner end. The presence of this latter feature in the type species is, however, considered as possibly due to *post-mortem* cracking of the exoskeleton. Eye ridge is apparently absent in the Builth specimen but this region of the cephalon is poorly preserved.

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The stratigraphy and brachiopods of the upper part of the type Caradoc of south Salop

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Synopsis

The type upper Caradoc rocks of south Salop are reviewed and a new lithostratigraphical and biostratigraphical scheme and revised chronostratigraphical nomenclature presented. Around the Onny Valley five formations are erected, in ascending order the Horderley Sandstone Formation, Alternata Limestone Formation, Cheney Longville Formation, Acton Scott Formation and Onny Shale Formation. The Cheney Longville Formation is divided into a lower Glynboro Member and an upper Crosspipes Member. The Acton Scott Formation is divided into a lower Ragdon Member and an upper Wistanstow Member in the immediate vicinity of the Onny Valley, but at Acton Scott the Henley Member calcareous sandstones replace most of the Wistanstow Member.

The sequence comprises five Caradoc Stages: Longvillian, Woolstonian, Marshbrookian, Actonian and Onnian. The Woolstonian is new and replaces the old Upper Longvillian Substage, whilst the Longvillian is redefined to replace the old Lower Longvillian Substage. The Marshbrookian/Actonian boundary is redefined to coincide with a major faunal turnover 10 m from the summit of the Crosspipes Member of the Cheney Longville Formation. North of the Stretton Hills, near Chatwall, the middle and upper Caradoc rocks differ from the southern sequence. Four formations are defined; in ascending order the Chatwall Sandstone Formation, Chatwall Limestone Formation, Cheney Longville Formation and Acton Scott Formation. This sequence ranges from Soudleyan to Actonian; no Onnian rocks are developed. Correlation between the northern and southern areas is difficult. A condensed sequence or non-sequence at the base of the Alternata Limestone Formation in the Onny Valley is not represented northwards. Correlation based on the identification of a transgressive impulse at the base of the Woolstonian in the Onny Valley suggests that the base of the Cheney Longville Formation at Chatwall may be slightly older than in the southern region, and the Chatwall Limestone Formation may be slightly older than the Alternata Limestone Formation, although their faunas are similar. Faunal lists are provided, including ranges, to facilitate correlation with the type area.

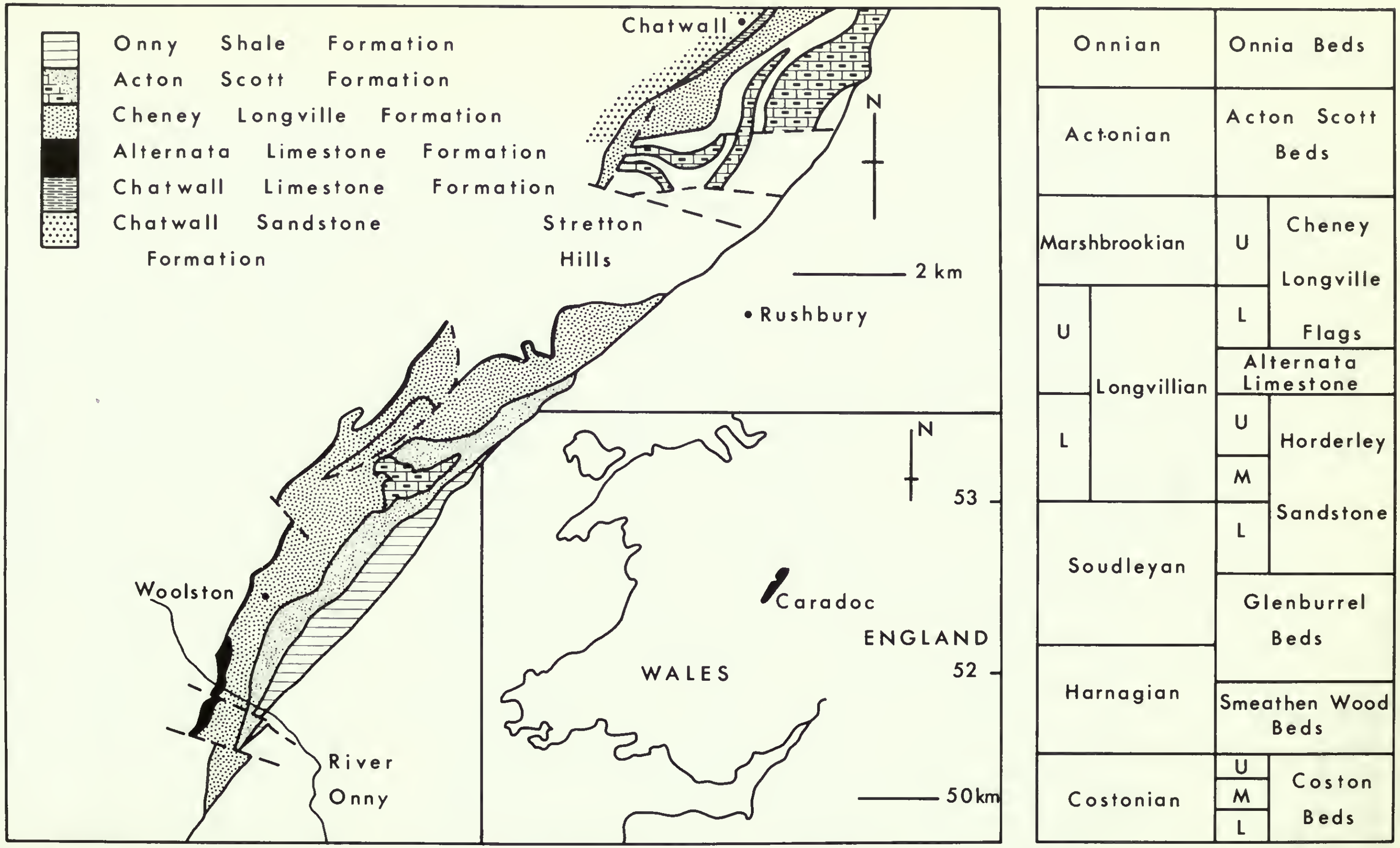
The brachiopod fauna, mainly internal moulds, consists of 63 species and subspecies – 17 Inarticulata, 31 Orthida, 14 Strophomenida and one Spiriferida. The following species are new: *Obolus salopiensis*, *Palaeoglossa lockleyi*, *Paracraniops doyleae*, *Schizocrania hewardi*, *Orbiculoidea ovata*, *Rhactorthis actoniae*, *Rhactorthis grandis*, *Bancroftina hewitti* and *Bancroftina whittingtoni*. New subspecies are *Dalmanella multiplicata prima* and *Dalmanella unguis ultima*.

Introduction

The abundant and well-preserved shelly fauna of the type Caradoc area, Salop (Fig. 1), represents a range of near-shore to off-shore environments and is ideal for the study of evolutionary ecology. However, before the ecology can be analysed successfully, it is necessary to revise the stratigraphy and also the systematics of the most common animal group – the Brachiopoda. This paper is chiefly concerned with the upper part of the type Caradoc succession, from the base of the Alternata Limestone upwards. However, in the area around Chatwall the stratigraphy of the middle Caradoc sediments is particularly complicated (Dean 1960*a*, Greig *et al.* 1968, Hurst 1979), and so it has been necessary there to revise the immediately underlying Longvillian strata as well. Dr M. G. Lockley is making a similar study of the older part of the type Caradoc.

Historical review

Murchison (1839) erected the name Caradoc for the Ordovician rocks of south-east Salop and applied the name Caradoc Sandstone to strata between the Wrekin and Coston (Figs 1 and 2).


Onny Shale Formation
Acton Scott Formation
Cheney Longville Formation
Alternata Limestone Formation
Chatwall Limestone Formation
Chatwall Sandstone Formation
Chatwall
N
Stretton Hills
2 km
Rushbury
Woolston
River Onny
N
53
Caradoc
ENGLAND
52
WALES
50km

Onnian			Onnia Beds
Actonian			Acton Scott Beds
Marshbrookian		U	Cheney Longville Flags
Longvillian	U	L	
			Alternata Limestone
	L	U	Horderley Sandstone
		M	
Soudleyan		L	
			Glenburrel Beds
Harnagian			
			Smeathen Wood Beds
Costonian		U	Coston Beds
		M	
		L	

Fig. 1 Outline geological map of the area between Chatwall and Cheney Longville, showing the upper Caradoc rocks. Inset map shows the location of the Caradoc district. The stratigraphical column indicates the main lithological and chronological subdivisions of the whole Caradoc sequence, prior to this work.

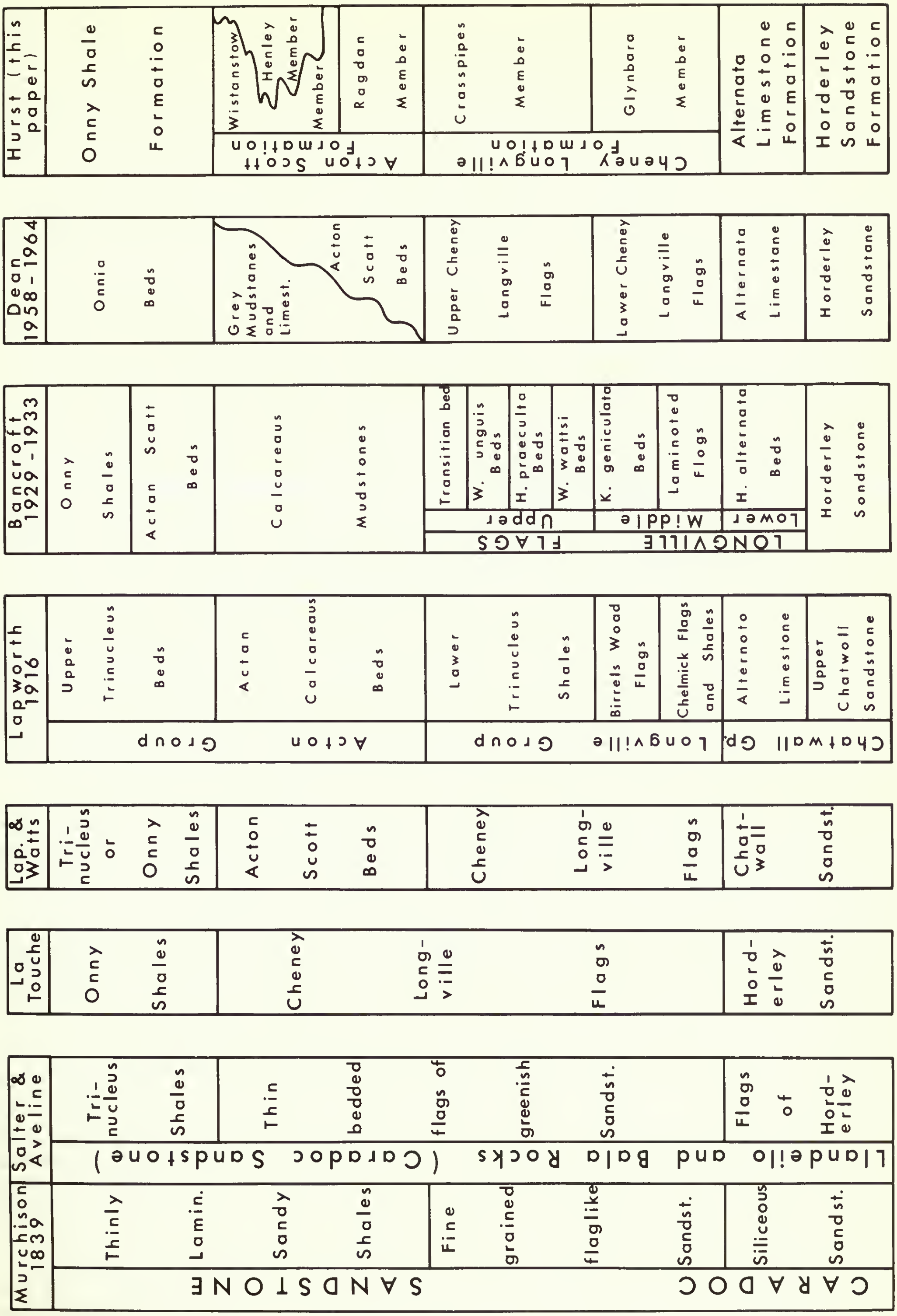

Murchison 1839
CARADOC SANDSTONE
Thinly Lamin. Sandy Shales
Fine grained flaglike Sandst.
Siliceous Sandst.
Salter & Aveline
Llandeilo and Bala Rocks (Caradoc Sandstone)
Tri-nucleus Shales
Thin bedded flags of greenish Sandst.
Flags of Hord-erley
La Touche
Onny Shales
Cheney Long-ville Flags
Hord-erley Sandst.
Lap. & Watts
Tri-nucleus or Onny Shales
Acton Scott Beds
Cheney Long-ville Flags
Chat-wall Sandst.
Lapworth 1916
Acton Group
Upper Trinucleus Beds
Acton Calcareaus Beds
Longville Group
Lower Trinucleus Shales
Birrels Wood Flags
Chelmick Flags and Shales
Chatwall Gp.
Alternoto Limestone
Upper Chatwoll Sandstone
Bancroft 1929-1933
Onny Shales
Actan Scatt Beds
Calcareaus Mudstones
LONGVILLE FLAGS
Upper
Transitian bed
W. unguis Beds
H. praeculta Beds
W. wattsi Beds
Middle
K. geniculata Beds
Laminated Flags
Lower
H. alternata Beds
Horderley Sondstone
Dean 1958-1964
Onnia Beds
Grey Mudstones and Limest.
Acton Scatt Beds
Upper Cheney Langville Flags
Lower Cheney Langville Flags
Alternata Limestane
Horderley Sandstane
Hurst (this paper)
Onny Shale Formation
Acton Scott Formation
Wistanstow Member
Henley Member
Ragdan Member
Cheney Longville Formation
Crosspipes Member
Glynbara Member
Alternata Limestone Formation
Horderley Sandstone Formation

Fig. 2 The main classifications and correlations of upper Caradoc strata.

He stated that the Onny Valley presented the best section and as can be seen from Fig. 2 an attempted subdivision of the strata was made. However this unit was far more comprehensive than Murchison probably intended, as subsequent researchers showed it to contain rocks Pre-Cambrian to Silurian in age. Later Ramsay & Aveline (1848) and Forbes (1848) still retained the Upper Llandovery rocks of the Longmynd area in the Caradoc. Not until the work of Sedgwick (1852) was there realisation of the inherent mixture in the Caradoc. He noted the trilobites *Ampyx* and *Trinucleus* near Cheney Longville and differentiated the 'Horderley' and 'May Hill' (now Upper Llandovery) Caradoc faunas, suggesting that the latter were younger.

Ramsay (1853) revised his earlier interpretation (Ramsay & Aveline 1848), connecting the Caradoc Sandstones of the Longmynd with the Wenlock Shales. This small paper heralded the major changes of the following year, in which Salter & Aveline (1854) published their classic results. They divided the revised Caradoc Sandstone into five parts, from youngest to oldest:

1. *Trinucleus* Shales
2. Thin-bedded flags of greenish sandstone
3. Thick-bedded flags of Horderley
4. Hoar Edge Grits
5. Shales of Harnage and Shineton.

The first three units are the ones dealt with here (Fig. 2).

Callaway (1877) differentiated the Caradoc Harnage Shales from the Tremadoc Shineton Shales, placing the former above the Hoar Edge Grits. He also proposed the name Chatwall Sandstone to replace the 'thick-bedded flags of Horderley' of Salter & Aveline. In 1884 La Touche introduced the names Onny Shales, Cheney Longville Flags and Horderley Sandstone corresponding respectively to units 1 to 3 of Salter & Aveline (Fig. 2). From this it is apparent that the Chatwall Sandstone and Horderley Sandstone are synonymous. Lapworth & Watts (1894) subsequently erected Acton Scott Beds for strata contained between the Onny Shales above and the Cheney Longville Flags below (Fig. 2). Cobbold (1901) recognized the *Alternata* Limestone for the first time but placed it in with the Chatwall or Soudley Sandstone. With the coining of the term Soudley Sandstone, there were three names for a single unit, i.e. Chatwall, Horderley and Soudley Sandstones.

Lapworth (1916) proposed the name Caradoc Series and divided the strata into a number of 'Groups' (Fig. 2). These 'Groups' were further subdivided, but no information regarding lithologies, faunas or type localities was offered. Nevertheless, Lapworth was the first person to recognize the heterogeneous nature of the Cheney Longville Flags by subdividing the unit into three.

Bancroft subdivided the type Caradoc Series into units characterized by the faunas, mainly of brachiopods and trilobites (Fig. 2). He first named the Soudleyan, Longvillian and Marshbrookian Stages in the predominantly sandstone units in the middle of the Series (1929*a*). Later the same year (1929*b*) he listed six stages for the whole Caradoc, in ascending order Girvanian, Harnagian, Soudleyan, Longvillian, Marshbrookian and Actonian (Fig. 1). At this point the youngest stage, the Onnian, was not introduced by name, although the subdivision was incorporated in his table. Bancroft also privately published a short paper in 1933, showing the vertical extent and lithological and faunal composition of the Stages Costonian to Onnian. The Costonian was not defined and was simply introduced as a replacement for the Girvanian (Fig. 1).

A paper published posthumously (Bancroft 1945) added more information regarding the Stages, but unfortunately they still remained ill-defined in terms of vertical extent. Further, many of the subdivisions were defined before the species of brachiopods and trilobites upon which they depended had been formally erected. These inconsistencies have marred Bancroft's work and made it difficult to follow. Nevertheless, as Dean (1958) indicates, Bancroft revolutionized stratigraphical research in the Ordovician. Not only did he collect faunas in bulk from single horizons, but he also tried to introduce statistical methods into his palaeontological work (Bancroft 1928*a*), and his methods far surpass many of today.

Dean (1958, 1960*a*, 1964) reviewed and revised the Stages and Zones of Bancroft based on a thorough redescription of the trilobite faunas (Dean 1960–63) and also published extensive faunal lists, but did not formally revise the lithostratigraphy (Fig. 2). He suggested that the name Acton Scott Beds *sensu stricto* should be reserved for the yellow calcareous sandstones of the

<table>
<tr><th colspan="3">CHRONOSTRATIGRAPHY</th><th colspan="2" rowspan="2">LITHOSTRATIGRAPHY</th><th colspan="2">BIOSTRATIGRAPHY</th></tr>
<tr><th colspan="2">Series</th><th>Stage</th><th>Brachiopods</th><th>Trilobites</th></tr>
<tr><td rowspan="7">CARADOC</td><td rowspan="6">Upper</td><td>Onnian</td><td colspan="2">Onny Shale Formation</td><td>Onniella Sericaidea</td><td>Onnia</td></tr>
<tr><td rowspan="2">Actonian</td><td rowspan="2">Acton Scott Fm.</td><td>Wistanstaw Member
Henley Member</td><td>Onniella Cryptathyris</td><td rowspan="2">Platylichas Chasmaps</td></tr>
<tr><td>Ragdan Member</td><td>Onniella Hedstraemina</td></tr>
<tr><td>Marshbrookian</td><td rowspan="2">Cheney Longville Fm.</td><td>Crasspipes Member</td><td>Dalmanella</td><td rowspan="3">Braeggeralithus</td></tr>
<tr><td rowspan="2">Woolstonian</td><td>Glynbara Member</td><td rowspan="2">Kjaerina Bancraftina Heterarthis</td></tr>
<tr><td colspan="2">Alternata Limestone Formation</td></tr>
<tr><td>Lr</td><td>Longvillian</td><td colspan="2">Horderley Sandstone Formation</td><td></td><td></td></tr>
</table>

Fig. 3 Revised stratigraphical classification of the type upper Caradoc Series.

Acton Scott district, whilst he referred to the time-equivalent division elsewhere simply as 'grey mudstones and limestones' (Dean 1958). The Geological Survey of Great Britain (Greig *et al.* 1968) essentially followed the previous nomenclatures, although they amalgamated all the facies of the Actonian into an Acton Scott Group, and did not subdivide the Cheney Longville Flags.

Lithostratigraphy: Cheney Longville to Soudley

The lithostratigraphical units recognized here are essentially those of Bancroft (1929*a*, *b*, 1933) and Dean (1958, 1964). However, it has proved desirable to revise some of the lithostratigraphic boundaries, as well as to formalize the nomenclature and to define boundaries precisely (Fig. 3). The stratigraphy of the Soudley to Cheney Longville area will be described first, followed by a short account of the Cardington – Chatwall district (Fig. 1).

a. Horderley Sandstone Formation

This formation immediately underlies the Alternata Limestone Formation from Soudley (SO 477918) to Cheney Longville (SO 415852). It has a maximum thickness of 180 m, in the Onny Valley (SO 415858), and consists of laminated and cross-bedded medium-grained sandstones (Fig. 16, p. 213). The basal beds are some 70 m thick and commence with laminated medium-grained sandstones which pass gradationally from the underlying Glenburrell Beds (Dean 1964). Interbedded shale units are common and may reach 10 cm in thickness. The middle part of the sequence is well exposed in the Long Lane Quarries (SO 413842) and the large Onny Valley Quarries (SO 415858), and consists of 50 to 60 m of massive, low angle cross-laminated or parallel-laminated medium-grained sandstone (Figs 19, 21). Shelly coquinas are common in the laminated sandstones, often reaching a thickness of 50 cm. The uppermost 30 or 40 m of this formation is only developed in the Onny Valley, and consists of parallel to very low-angle cross-laminated medium-grained sandstone. Interbedded thin bioturbated fine sandstones (*c.* 5 cm) occur in the upper 5 m and form a transition into the overlying Alternata Limestone Formation.

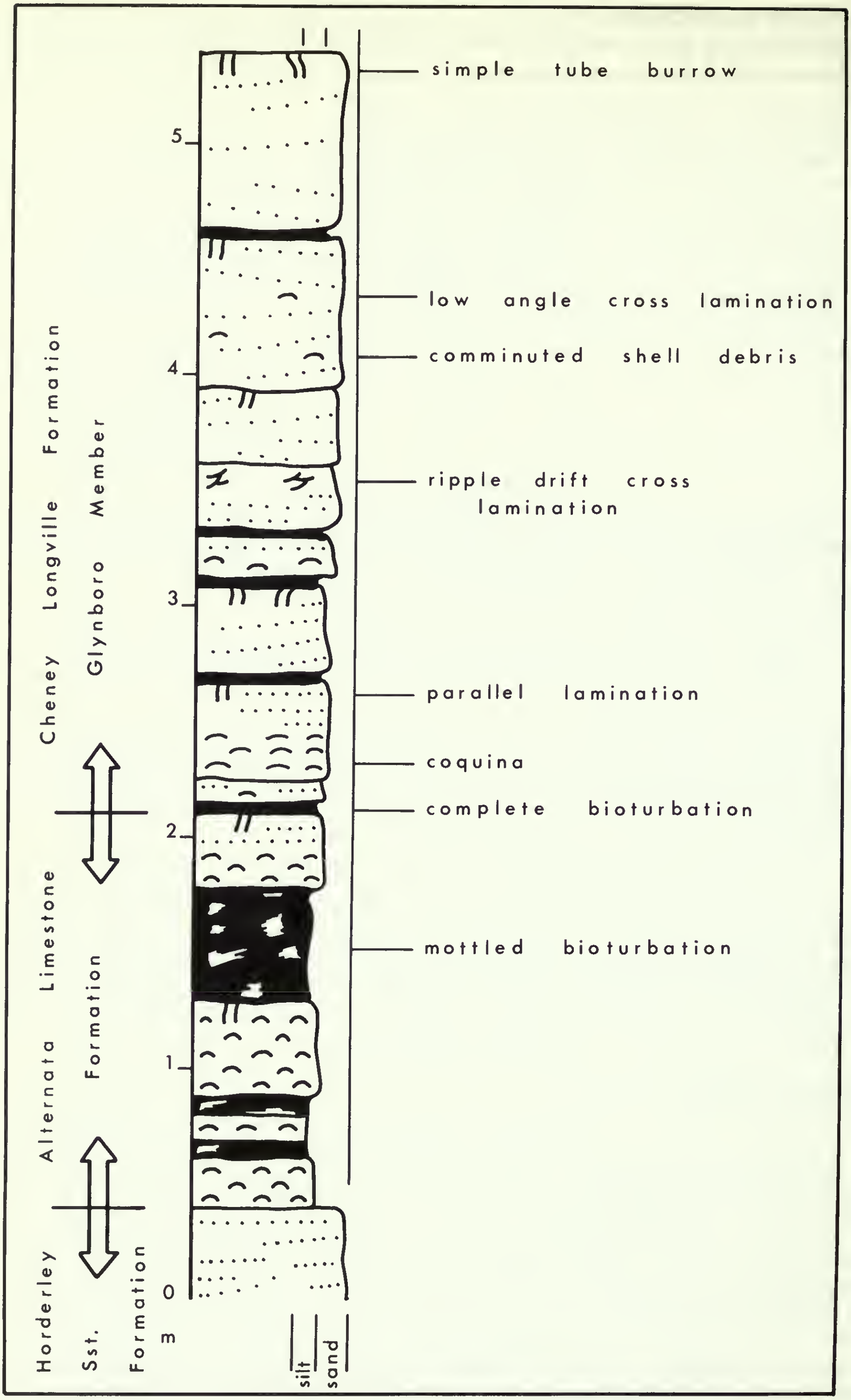

simple tube burrow
low angle cross lamination
comminuted shell debris
ripple drift cross lamination
parallel lamination
coquina
complete bioturbation
mottled bioturbation
Cheney Longville Formation
Glynboro Member
Alternata Limestone Formation
Horderley Sst. Formation
5
4
3
2
1
0
m
silt
sand

Fig. 4 Sedimentological log of the boundary between the Alternata Limestone Formation and Cheney Longville Formation at Soudley Quarry, SO 477918.

To define a lower lithological boundary to this formation, or to subdivide it, is outside the scope of this paper. However, an upper boundary is defined since it is also the base of the Alternata Limestone Formation.

Some 10 m west of a footbridge across the Onny River (SO 418856) the contact between the Horderley Sandstone Formation and the Alternata Limestone Formation is exposed. The top of the Horderley Sandstone Formation is defined at the base of the first thick shelly limestone influx (coquina) containing *Heterorthis alternata*, *Trematis punctata* and occasional phosphatic nodules and fossils (see Fig. 12, p. 202). In this section the initial coquina is some 50 cm thick, and occurs on both sides of the river bed. This section is also described below as the standard section for the base of the Woolstonian Stage (Fig. 12).

North of the Onny Valley in Marshbrook Railway Cutting (SO 440905) a faulted outcrop of the Horderley Sandstone Formation and Alternata Limestone Formation is seen. The contact is not now accessible (see Hurst 1979), but from the available exposure the Horderley Sandstone Formation does not appear to be as complete as in the Onny Valley. It consists of approximately 15 m of laminated medium-grained purple or greenish sandstone with thin shelly lenses along the laminae and with occasional pebble stringers 1 cm thick. These sediments are most similar to the middle or upper part of the Onny Valley sequence and there does not appear to be a gradation into sediments typical of the upper Horderley Sandstone Formation of the Onny Valley or into the overlying Alternata Limestone Formation.

At Soudley Quarry (SO 477918) parallel-laminated medium-grained purple and green sandstones with occasional thin shelly layers (Fig. 16) are overlain by the Alternata Limestone Formation (Hurst 1979). This is presumably one of the localities that prompted Cobbold (1901) to refer to a 'Chatwall or Soudley Sandstone'. As Dean (1960*a*) has demonstrated and will be discussed later, the Chatwall Sandstone is a lithostratigraphic unit distinct from the Soudley Sandstone. However, there is no lithological difference between the Horderley Sandstone Formation and Soudley Sandstone. Thus the term Soudley Sandstone is abandoned in favour of the Horderley Sandstone Formation, which has priority.

b. Alternata Limestone Formation

This stratum is named after the brachiopod *Heterorthis alternata* which occurs abundantly in shelly limestone lenses (Fig. 24). Cobbold's name (1901) is retained because the index species *Heterorthis alternata* is the type-species of the genus and the Alternata Limestone Formation includes the type-locality for the species.

The Alternata Limestone Formation consists of a series of interbedded bioturbated silty shales and sandy silts (c. 10 cm), laminated and graded fine sandstones often with a basal shell lag (10 to 50 cm thick), and thick shelly limestone bands (Fig. 22). The latter can be 50 cm thick, and consist of packed coarse shell material set in a matrix of sandy silt. The shells show no signs of grading or preferred orientation, but the beds appear crudely laminated owing to the alignment of large flat shells of *Heterorthis alternata* and *Kjaerina bipartita* (Fig. 24).

As Dean (1958, 1964) pointed out, this formation is a useful mapping horizon at the base of the Cheney Longville Formation. Nowhere does it exceed 30 m in thickness, and its maximum development is at Woolston (SO 423873). Between the roadside exposure west of Cheney Longville (SO 416852) and the Onny Valley (SO 418856 and SO 418857) it maintains a thickness of approximately 20 to 25 m. At Marshbrook (SO 440905) only some 15 m are exposed but its true thickness is probably greater than this. Only 2 m of Alternata Limestone Formation occurs at Soudley Quarry (SO 477918). This small thickness, and the fact that phosphatic nodules and phosphatized fossils also occur, suggests a condensed sequence (Fig. 16). Between Soudley and Cheney Longville it is only the basal metre of the succession which contains phosphatized fragments. An analysis of the facies changes at this horizon, with detailed sections, are given by Hurst (1979). Discussion of section correlations of the uppermost Horderley Sandstone Formation and Alternata Limestone Formation are given later under Chronostratigraphy, p. 210.

Soudley Quarry (SO 477918) is the only place where the contact of the Alternata Limestone Formation and the Cheney Longville Formation is seen. This is not the ideal locality to define the junction of these two formations. However, in the Marshbrook (SO 440905), Woolston (SO

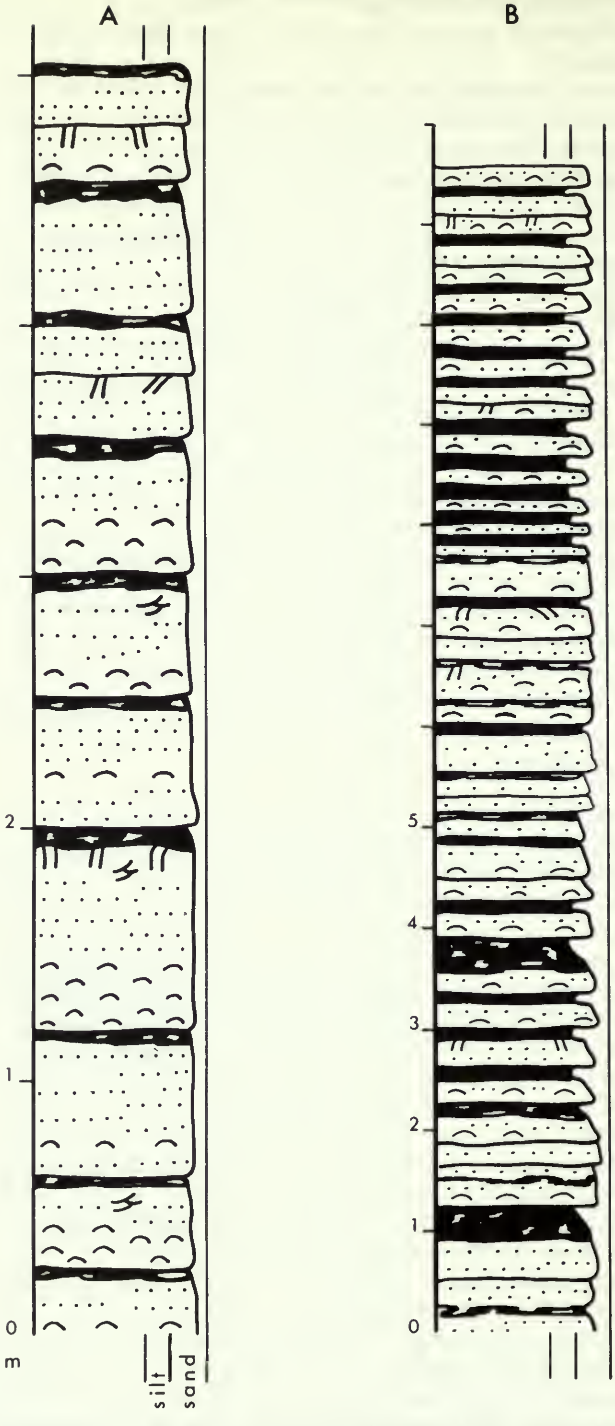


Fig. 5 Examples of sedimentary logs of the Glynboro Member of the Cheney Longville Formation, from (A) the stream section at Soudley SO 478916 and (B) the old river cliff locality in the Onny Valley at SO 422890. Symbols explained in Fig. 4.

423873) and Onny Valley (SO 418857) sections there is a gap, of 5 to 10 m stratigraphically, between the highest undoubted Alternata Limestone Formation exposure and lowest strata of the Cheney Longville Formation. As can be seen from Fig. 4, p. 190, the basal Cheney Longville Formation is readily distinguishable from the Alternata Limestone Formation. The top of the latter is taken to coincide with the top of the last thick shelly limestone coquina with abundant *Heterorthis alternata*. Above this the Cheney Longville Formation is characterized by the absence of shelly lenses, and the sediment is also slightly coarser.

c. Cheney Longville Formation (Figs 17, 18, 20)
The Cheney Longville Formation is an homogeneous sequence of sands, silts and sandy silts, some 180 to 200 m thick and weathering greenish-yellow. It was originally named by La Touche (1884), Fig. 2. Two members are recognized.

Glynboro Member. The basal member, named after the cottage of Glynboro (SO 418859) in the Onny Valley, corresponds precisely to the Lower Cheney Longville Flags of Dean (1958). It comprises approximately 120 m of buff yellowish to olive green weathering siltstones and sandstones. Sandstone beds 10 to 50 cm thick are interbedded with 20 cm bioturbated sandy silt units (Fig. 17). The sandstone beds are graded and have planar erosive bases and occasionally a persistent basal coquina which gradationally passes up into parallel or very low-angle cross-lamination. The bioturbated horizons account for approximately 10% of the succession in the lower half of the Member and up to 25% in the upper part. The fauna is best in the coquinas, but occurs as comminuted debris throughout. A very sparse fauna occurs in the bioturbated horizons and is the same species as in the shell beds. An example of a sedimentary facies log of this member is shown in Fig. 5 (see also Hurst 1979).

The base of the Glynboro Member and the Cheney Longville Formation is defined at Soudley Quarry (Fig. 4). Very few good sections exist in the lowest part of this Member, the most extensive being in the stream section (SO 478916) south-west of Soudley Quarry (see Hurst 1979). Poor sporadic exposures occur in the lane west of Cheney Longville and in the Onny Valley. The higher beds are better represented. An almost continuous laneside exposure due west of Cheney Longville (SO 418851) includes the transition into the overlying Crosspipes Member. Further limited exposures occur at Woolston, and in an old cart track at Whittingslow (SO 436892) there is another continous exposure into the Crosspipes Member. An extensive section is present in an old river cliff in the Onny Valley (SO 422890).

Crosspipes Member. This member, named after Crosspipes Farm (SO 429892), comprises a maximum of 60 m and corresponds to the Upper Cheney Longville Flags of Dean (1958). It consists of thin laminated and graded very fine sandstones (*c*. 10–15 cm) interbedded with thick (up to 50 cm) bioturbated sandy and silty shales (Figs 18, 20). The tops of the fine sandstone beds are penetrated by simple tube burrows and grade into the overlying bioturbated units. Fauna is abundant in the bioturbated units and the same species occur concentrated as lensing shell lags at the base of the laminated sandstones (Fig. 25). Some lenses are up to 15 cm thick and are persistent. Occasionally in the bioturbated silty shales thin lenses of small fragments of volcanic glass, pumice and orthoclase feldspar crystals can be traced across the outcrop.

The thickness of the laminated fine sandstones decreases quickly up through the member until the top 10 or 15 m consists primarily of bioturbated and partially bioturbated sandy silts and sandy shales. Shell concentrations up to 5 cm thick become common in the top 10 m of strata, but they are not associated with laminated graded sand units (Fig. 18). Fig. 6 gives examples of sedimentary logs from this member.

The Crosspipes Member (lowest part) is well exposed at the motte and bailey at Cheney Longville (SO 419849), in an extensive river section in Marshwood (SO 442891) and a river section near Ragleth Hill (SO 451908).

The base of the Crosspipes Member, and thus the top of the underlying Glynboro Member, is taken in a fairly continuous roadside exposure at Cheney Longville (SO 418851 to SO 419849), and coincides with the stage boundary between the Woolstonian and the Marshbrookian (Fig. 13,

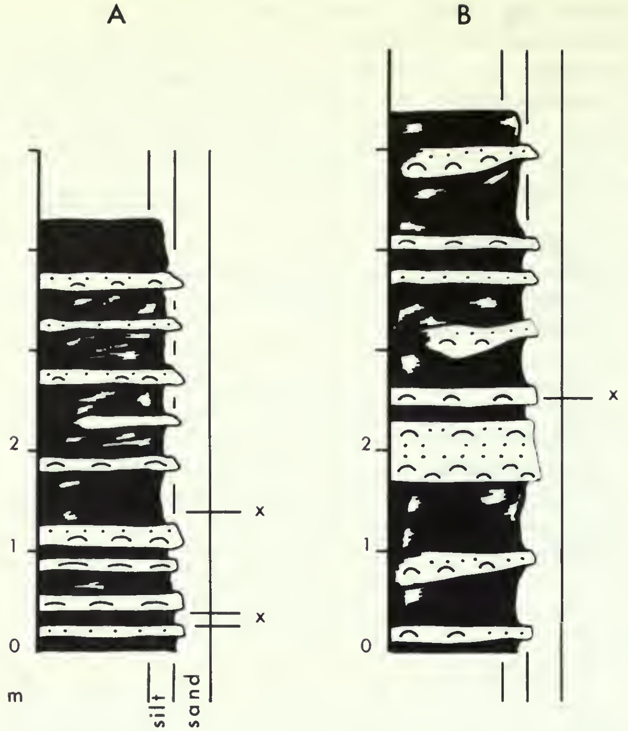


Fig. 6 Examples of sedimentary logs of the Crosspipes Member of the Cheney Longville Formation, from (A) the Minton road section at SO 439900 and (B) the stream section in Marshwood at SO 422891. Symbols explained in Fig. 4.

p. 203). The lithological boundary between the two members is gradational over several metres. The base of the Crosspipes Member is taken at the increase in thickness of bioturbated units intercalated with thin laminated sandstone beds. This change is also accompanied by a decrease in sediment grain size from predominantly sands and sandy silts to silts and silty shales (Fig. 20). The fauna is also more abundant in the Crosspipes Member.

d. Acton Scott Formation

In the Onny Valley above the Cheney Longville Flags and below the Onny Shale Formation (Fig. 3) the sequence consists of two basic facies, a siltstone below and a calcareous siltstone above. However, to the north, around Acton Scott, the siltstones are succeeded by hard calcareous sandstones. Each of these three divisions is defined here as a member.

Ragdon Member. Named after the village of Ragdon (SO 458915), this comprises approximately 30 m of mottled (intensely bioturbated) siltstones, weathering buff to green. Occasionally burrow-disrupted current laminae occur, and non-bioturbated primary bedding accounts for about 2% of the succession. Isolated laminated siltstone beds with a basal layer of shell debris occur rarely. The rich and diverse fauna is distributed randomly throughout the sequence, although paper-thin layers of bedding-parallel shell fragments and convex-upward shells (not associated with laminated silts) occur at a frequency of about one layer per 5 m (Fig. 26).

This member weathers easily to form low-lying land, and as a result is poorly exposed, mainly in overgrown stream sections. It is not exposed south of the Onny Valley; a stratigraphically low but poor exposure under a tree in an abandoned meander of the river is the most southerly outcrop (SO 423854). Two small outcrops in the middle part of the member occur on the north side of the river in a roadside bank (SO 424855) and in an overgrown valley known as Dandy Hollow

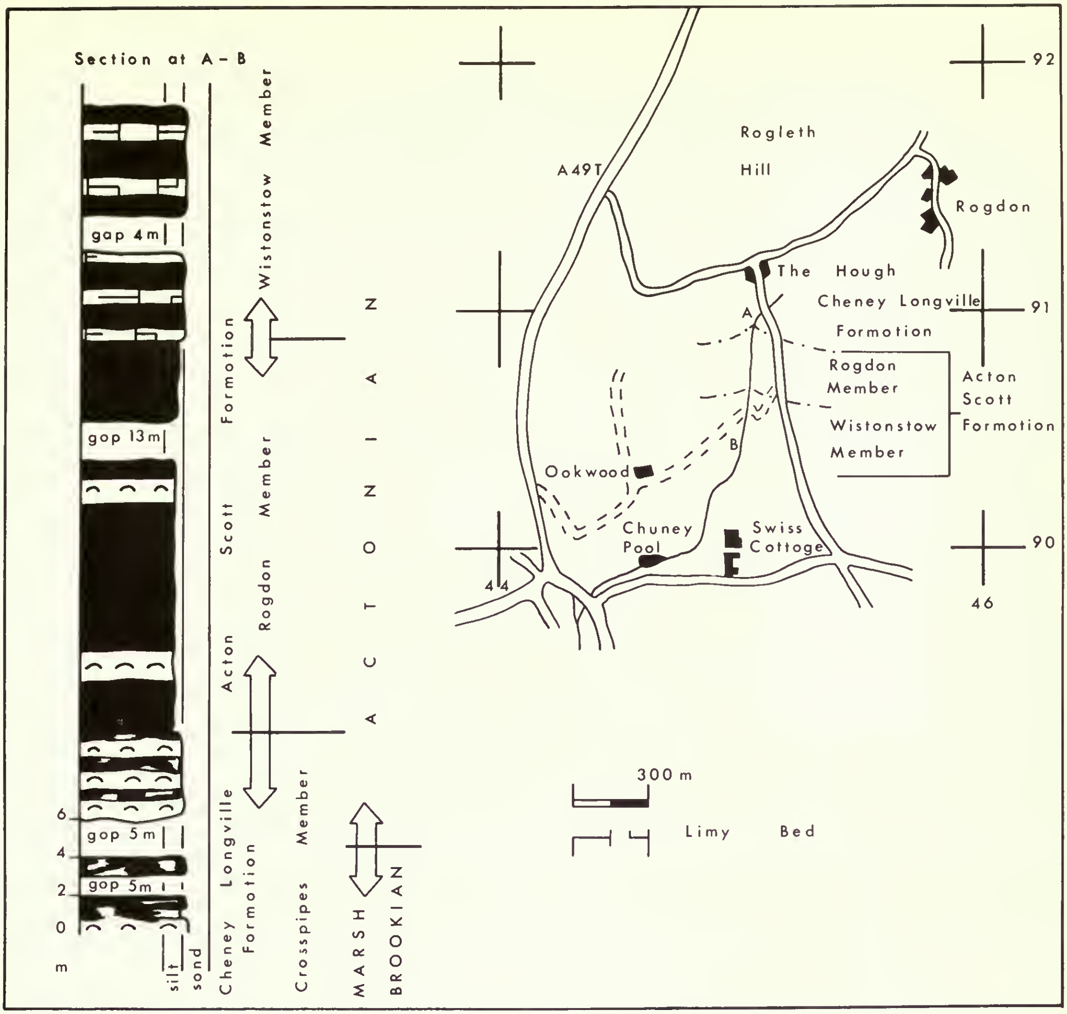

Section at A – B
gap 4m
gap 13m
gap 5m
gap 5m
6
4
2
0
m
silt
sand
Cheney Longville Formation
Crosspipes Member
Acton Scott Formation
Ragdon Member
Wistanstow Member
MARSH BROOKIAN
ACTONIAN
A49T
Ragleth Hill
Ragdon
The Hough
A
B
Cheney Longville Formation
Ragdon Member
Wistanstow Member
Acton Scott Formation
Oakwood
Chuney Pool
Swiss Cottage
92
91
90
44
46
300 m
Limy Bed

Fig. 7 Location of the stratotype boundary between the Cheney Longville Formation (Crosspipes Member) and the Acton Scott Formation (Ragdon Member), and between the Ragdon and Wistanstow Members of the Acton Scott Formation. Symbols explained in Fig. 4.

(SO 425858). Dean (1958) reported that in Marshwood Quarry (SO 445890) the transition from the Cheney Longville Formation to the Acton Scott Formation could be examined in the cart track to the south, but this is not possible now as the section is overgrown. In the vicinity of Acton Scott there are stream exposures at Ragleth Hill (SO 451906), west of Hatton (SO 465901) and at Chuney Pool (SO 466899).

The only exposure of the transition from the Cheney Longville Formation (Crosspipes Member) to the Acton Scott Formation (Ragdon Member) is in a stream section near Oakwood south of Ragleth Hill (SO 451908 to SO 451906), and this is considered the stratotype between the two formations and their members (Fig. 7). The boundary is gradational over a couple of metres, the sediment grain size changing from a sandy silt to a muddy silt. The boundary is taken at the beginning of the finer-grained sediments, which are more mottled and thoroughly bioturbated. This transition is accompanied by a loss of distinct shelly layers (Fig. 7). Detailed work by Bancroft in the Onny Valley indicated a complete section in this interval (SO 422854). However, the section is not now so clean (see Fig. 8), but various small pits were dug and a similar transition as described for the type section was verified.

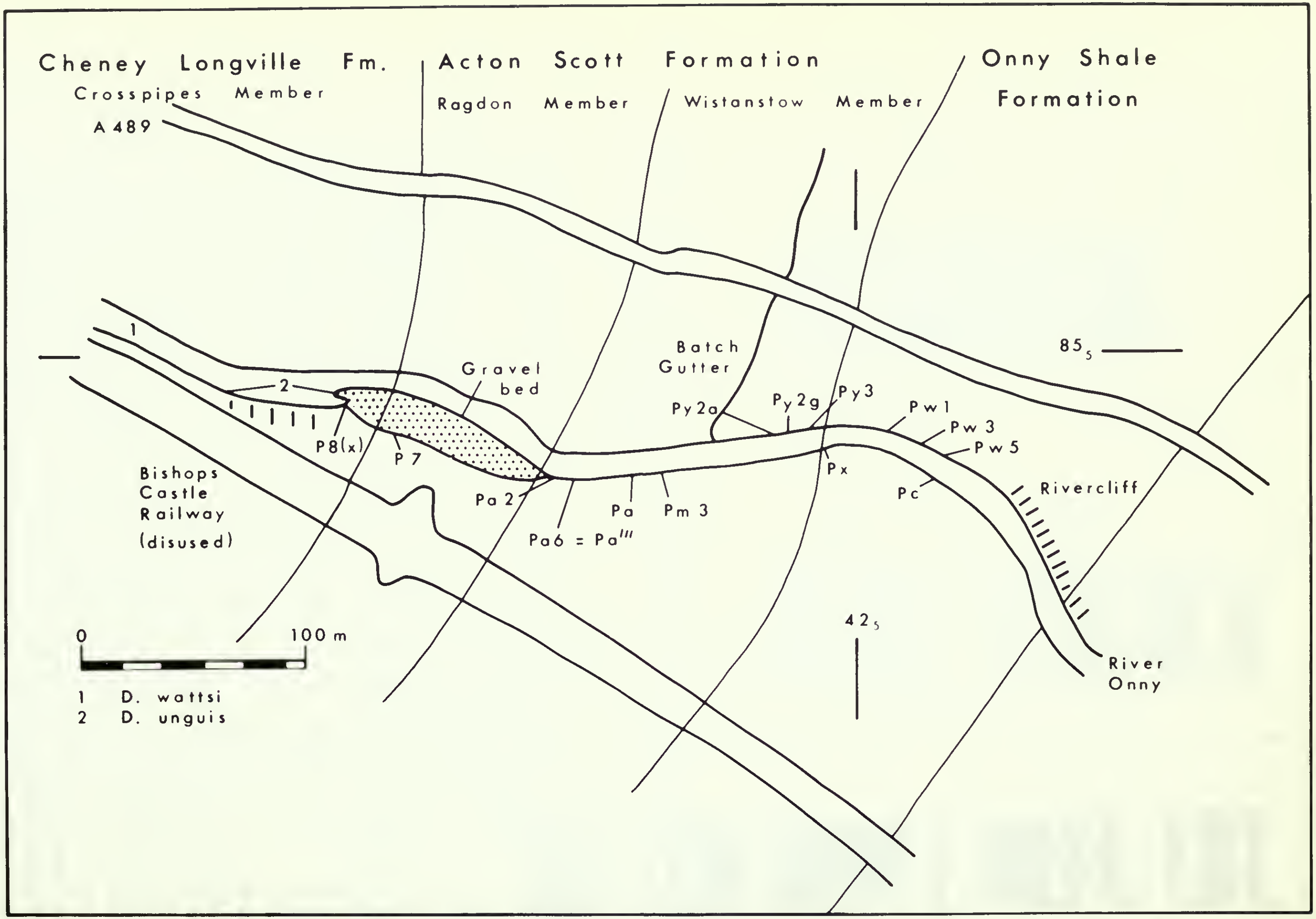

Cheney Longville Fm.
Crosspipes Member
Acton Scott Formation
Ragdon Member
Wistanstow Member
Onny Shale Formation
A 489
1
2
Gravel bed
Batch Gutter
Py2a
Py2g
Py3
Pw1
Pw3
Pw5
P8(x)
P7
Pa2
Pa6 = Pa'''
Pa
Pm3
Px
Pc
Rivercliff
85₅
42₅
River Onny
Bishops Castle Railway (disused)
0
100 m
1 D. wattsi
2 D. unguis

Fig. 8 Upper Caradoc exposures in the Onny Valley section. The numbered localities are from Bancroft (1949), most of which are still extant, except for P8(x) and Px. The point between Py3 and Px marks the stratotype between the Acton Scott Formation (Wistanstow Member) and the Onny Shale Formation as well as between the Actonian and Onnian Stages.

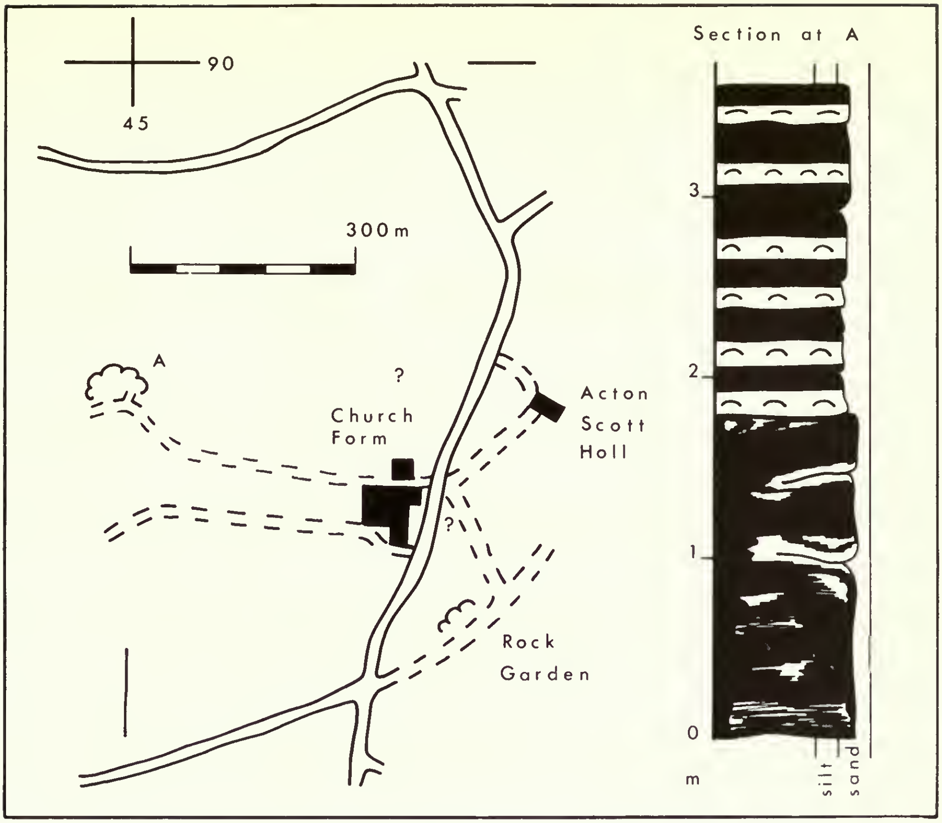


Fig. 9 Location and section of the stratotype for the Henley Member of the Acton Scott Formation. Symbols explained in Fig. 4. Question marks indicate filled-in quarries.

Wistanstow Member. Named after the village of Wistanstow 500 m north of the Onny Valley, this consists of some 40 m of thoroughly bioturbated yellowish to blue weathering calcareous siltstones and blue-black silty mudstones. Gradational silty blue limestone bands and nodules occur throughout. Generally the fauna is of low diversity although occasional thin bedding planes contain locally concentrated convex-upward shells.

Near Acton Scott the member is far more silty and contains thick (*c*. 10–15 cm), hard, somewhat nodular blue limestone bands (Fig. 7). In the stream section south of Ragleth Hill (SO 451905) some 5 to 10 m is exposed above the Ragdon Member, and a similar smaller sequence is exposed at the top of the section in the river west of Hatton (SO 465901). In the Onny Valley the sediments are finer and consist of silty muds (see Fig. 8). Persistent limestone bands are not present, but scattered discrete nodules are common. Dean (1958) reported blue calcareous mudstones in a stream section at Ticklerton (SO 479910), which belong to the Wistanstow Member and which Dean considered to be middle Actonian.

The base of the Wistanstow Member is only exposed in the stream section at Oakwood (SO 451908 to SO 451906), and this is made the type locality for the junction between the Ragdon and Wistanstow Members of the Acton Scott Formation (Fig. 7). The sediment grain size is somewhat gradational over a metre, changing from muddy silts to sandy silts. However the base is defined by the incoming of thick, conspicuous, blue limestone bands which can be traced across the outcrop. They contain a rich fauna but the intervening bioturbated beds are only sparsely fossiliferous.

Henley Member. This unit, named after the village of Henley (SO 451883), is a hard calcareous sandstone which forms the high ground around Acton Scott. The beds immediately above and below the sandstone are not exposed and its thickness is not precisely known, although Greig *et al.* (1968) estimated it to be about 25 m.

The type section for this unit is taken to be the old quarry west of Acton Scott (SO 449896). Here some 5 or 6 m of massive yellow-weathering calcareous medium-grained sandstone, with a low diversity and density fauna, is succeeded by thinly-bedded bioturbated calcareous sandstones above (Fig. 9). The fauna in the upper unit is very diverse and commonly concentrated along thin bedding planes. Other exposures of this unit include the rock garden at Acton Scott Hall (SO 454893). Here the sandstone is lithologically different from the type section in that it is more muddy, resulting in a general blue colour. The boundaries of the member are not exposed.

e. Onny Shale Formation

This formation is a distinct lithological unit at the top of the Caradoc succession. The name Onny Shale is preferred to *Onnia* Beds of Dean (1958) not only because it has priority but also because it can be recognized on lithological grounds alone. The formation only outcrops in the Onny Valley (see Fig. 8) and consists of approximately 45 m (exposed) of mudstones at the type section (SO 425854 to SO 426854), which fall into three facies.

a. 20 m of bioturbated blue-black mudstones with individual lithified burrows. Some small pyritic nodules occur. A low-diversity but dense fauna is present, but is often crushed owing to sediment distortion.

b. 5 m of laminated blue-grey shale occurring in the river bed, just before the famous river cliff section (SO 426854) which forms the uppermost facies. It is similar in texture and composition to the mudstones, except that bioturbation is absent or restricted to single tube burrows. Laminations are on a millimetre scale and are defined by variations in the mud, silt and clay content of the sediment. Benthic fauna is extremely rare, but pelagic graptolites occur.

c. The river cliff section which consists of yellow-weathering blocky mudstones with restricted benthic fauna.

3 m is not exposed at the junction of the Acton Scott Formation (Wistanstow Member) and the Onny Shale Formation (Fig. 8). This (SO 425854) is taken as the type section for the boundary and within the missing sequence the poorly fossiliferous nodular calcareous muds and silts of the Wistanstow Member are replaced by the bioturbated blue-grey, pyritic, very fossiliferous muds of the basal Onny Shale Formation. The top of this formation is unconformably covered by the Llandovery.

Lithostratigraphy: Cardington to Chatwall

North of the Stretton Hills the lithostratigraphical succession of the middle, and parts of the upper Caradoc succession are different from the southern area. Dean (1960*a*) presented a detailed analysis of the Caradoc strata up to and including the *Alternata* Limestone. The succession he employed for this interval is as follows.

	Cheney Longville Flags
Upper Longvillian	*Alternata* Limestone
	unconformity
Lower Longvillian	Chatwall Sandstone
	unconformity
	Chatwall or *Glyptocrinus* Flags

Dean's unconformities are based entirely on faunal evidence and represent missing faunal assemblages (zones) compared with the Onny Valley section. Hurst (1979) has analysed the environment of deposition of the Alternata Limestone Formation and suggested that the unconformities may not be present. The evidence for this is discussed later under section correlation, p. 216. Only the strata above and including the Chatwall Sandstone are dealt with here, and a different lithostratigraphical nomenclature is required for this area, reflecting localized sedimentation patterns, a point also emphasized by Dean (1958, 1960).

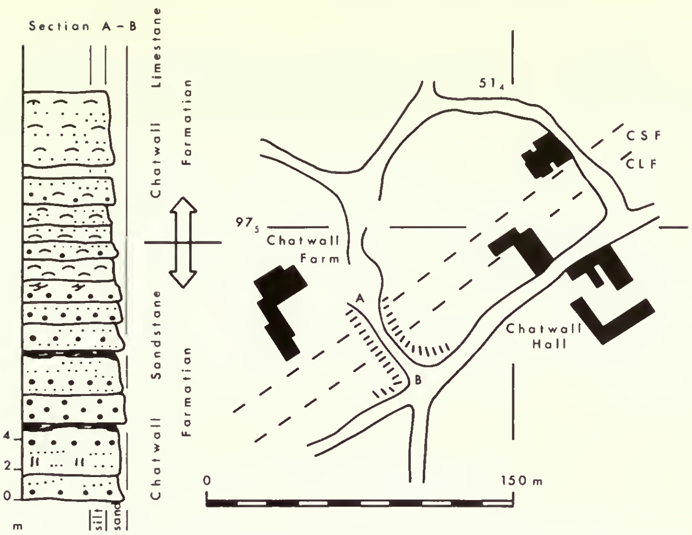


Fig. 10 Location and stratotype section for the Chatwall Sandstone and Chatwall Limestone Formations. Symbols explained in Fig. 4.

a. Chatwall Sandstone Formation

The Chatwall Sandstone Formation (Callaway 1877) is regarded as distinct from the Horderley Sandstone Formation and the name is used for strata north of the Stretton Hills (Fig. 1). The type section is taken in the lane to the south-west of Chatwall Hall (SO 514974), where are exposed some 18 m (Fig. 10) of lensing units of pebble conglomerates up to 100 cm thick, which are persistent across the outcrop. These pass sharply upwards into buff yellow, planar or low-angle cross-laminated, medium coarse sand units up to 150 cm thick. Some mottling is present (bioturbation) but body fossils have not been found in the lower 12 m, although Dean (1960*a*) reported occasional fragments. The uppermost 1 or 2 m has a fauna concentrated in shell lags. Pebble beds decrease in thickness and frequency into the upper part of the formation.

This definition of the Chatwall Sandstone Formation includes the lower 10 m which Dean (1960*a*) placed in the Chatwall Flags. The unit is exposed in numerous roadside cuttings, as the pebble beds form hard bands (SO 502965, SO 497961), and in some small quarries (SO 498962). The sandstone is hard and between Cwms and Chatwall caps an escarpment, but no base can be defined as exposure of this level is lacking.

b. Chatwall Limestone Formation

Formerly called the *Alternata* Limestone, it is not only readily distinguishable, lithologically, from the underlying Chatwall Sandstone Formation but also from the redefined Alternata Limestone Formation of the Soudley and Onny Valley region.

The type section is also located in the lane at SO 514974, where the limestone lies directly on the Chatwall Sandstone Formation (Fig. 10). The limestone consists of a matrix of medium-grained yellow sandstones which occur in laminated beds up to 50 cm thick. Fauna is common and concentrated in the base of individual beds or scattered throughout a unit. In many beds the shelly concentrates are so common as to form limestone bands. Occasional pebbles occur in the coquinas or are scattered along the laminae. Bioturbation is absent.

The base of the Chatwall Limestone Formation is defined in the lane section, and the transition is gradational over a metre. The base is taken at the first thick shelly coquina which contains *Heterorthis alternata*, accompanied by a reduction in sediment grain size and a loss of persistent pebble bands (Fig. 10). Away from the type section the limestone is now poorly exposed apart from a quarry in The Wilderness (SO 489956). A top to the Chatwall Limestone Formation cannot be defined as no suitable exposure exists.

c. Strata above the Chatwall Limestone Formation

In this northerly area the Cheney Longville Formation follows the Chatwall Limestone Formation, but it is very poorly exposed; the exposures that do exist confirm a similar sequence to the Soudley to Cheney Longville area.

The highest beds of the district belong to the Acton Scott Formation. Pocock & Whitehead (1948) stated that Lapworth's Acton Group did not occur north of the Cardington Hills. However, as Dean (1958) pointed out, the faunas recorded by Salter & Aveline (1854), from a fossiliferous locality near Gretton, indicate Actonian strata. More recently Greig *et al.* (1968) have reported some 160 m of strata which they refer to the Acton Scott Group, and which consists of two yellow flaggy shelly sandstones interbedded with mudstones. These beds are also considered here as the Acton Scott Formation, but the poor exposures preclude the erection of members. The increase in thickness of the formation from the Onny area is owing to the two sandstones which are lithologically similar to the Henley Member; the flaggy nature refers to the lamination. The reported fauna is also very similar.

Biostratigraphy

Bancroft (1928*b*, 1929*a*, *b*, 1933, 1945, 1949) revolutionized Caradoc stratigraphy by his erection of zonal schemes based on trilobites and brachiopods. Dean (1958) has revised some of this work, but without taxonomic revision of the brachiopods. Brachiopods are numerically the most important invertebrate group throughout all the formations (Hurst & Hewitt 1977) and the present revision of their taxonomy necessitates changes. As with the trilobites, genera often have fairly long ranges so that specific identification is critical.

The table at the end of this section (p. 207) shows the stratigraphical ranges of all the invertebrate species encountered in the upper Caradoc succession. It is suggested that the previous zonal schemes be abandoned (see Fig. 11). The concept of many of the brachiopod species is now radically different and many of the species names used by Bancroft are invalid. Over-emphasis of one particular species is also dangerous for correlation purposes. For these reasons the overall fauna should be used and in fact there are many faunal turnovers which not only reflect events controlled by ecological changes, but may be useful in correlation. Nevertheless, it is interesting that most of the zones of Bancroft (1933) do not simply reflect shifts of one or two species, but mirror major benthic events, affecting whole faunas. Characteristic species of upper Caradoc trilobites are shown in Figs 27–41.

The fauna of the Alternata Limestone Formation is dominated by brachiopods, which constitute upwards of 90% of the individuals. *Heterorthis alternata*, *Sowerbyella sericea*, *Trematis punctata*, *Bancroftina typa* and *Kjaerina bipartita* are the most common species, whilst trilobites are mainly represented by *Broeggerolithus longiceps*, *Kloucekia* (*Phacopidina*) *apiculata* and *Brongniartella bisulcata*. *Chasmops extensus* appears for the first time. The majority of the fauna occurs in shell beds and there is some indication that *H. alternata* and *T. punctata* occur together preferentially in particular beds (Hurst 1979). The total fauna is not diverse, which is not surprising as the sediments indicate nearshore environments (Hurst 1979). The abundance of both *H. alternata* and *T. punctata* forms a very useful marker horizon. The assemblage differs from the fauna in the uppermost Horderley Sandstone Formation (Onny Valley *sensu stricto*) in having these two species and also a far greater abundance of *Kjaerina bipartita*, which is of greater size in the Alternata Limestone Formation. *S. sericea* dominates the whole fauna of the underlying formation, whereas in the Alternata Limestone Formation it is not as common. The trilobite fauna is also different, with the main species in the Horderley Sandstone Formation being *Broeggerolithus globiceps*, *Brongniartella minor* and *Flexicalymene* (*Reacalymene*) *horderleyensis*. The latter two are rare, but the former is not uncommon.

The Glynboro Member of the Cheney Longville Formation contains two distinct faunal units. In the lower half the fauna is mainly left over from the preceding Alternata Limestone Formation, without *H. alternata* and *T. punctata*. The most abundant species are *Bancroftina typa* and *K. bipartita*. *S. sericea* again decreases in importance but the trilobite fauna is the same as previously,

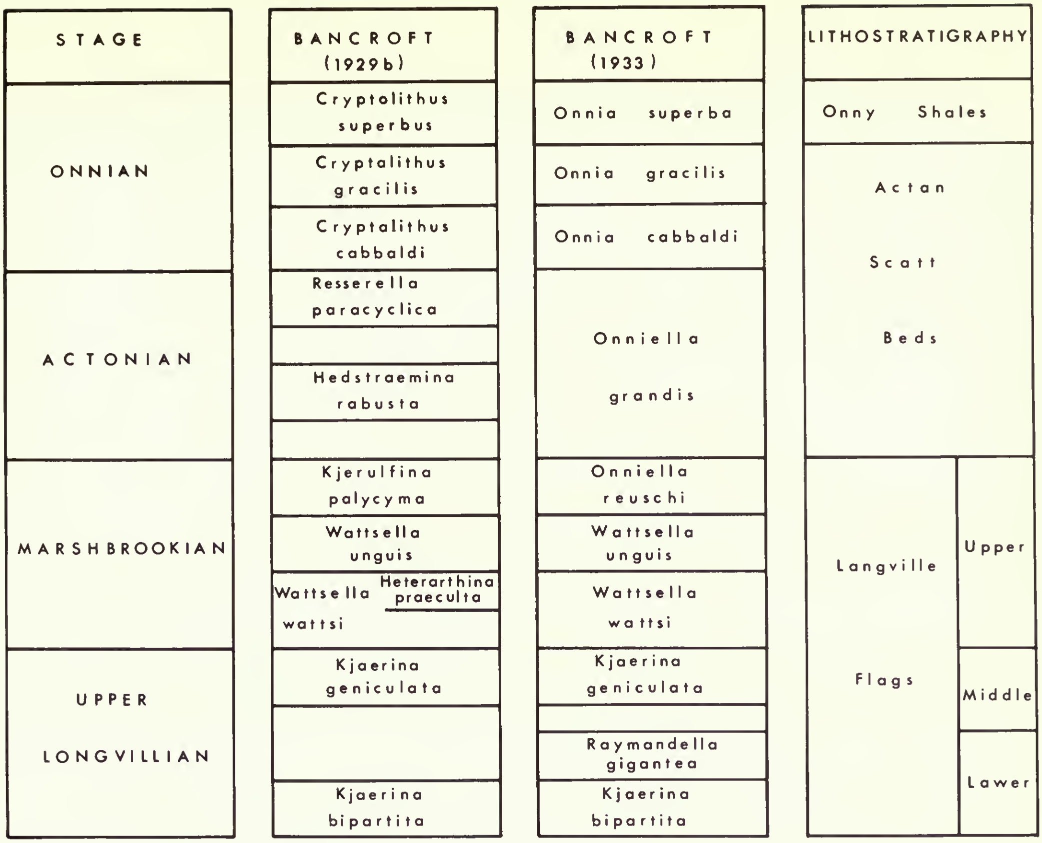

STAGE
BANCROFT (1929b)
BANCROFT (1933)
LITHOSTRATIGRAPHY
ONNIAN
ACTONIAN
MARSHBROOKIAN
UPPER LONGVILLIAN
Cryptolithus superbus
Cryptalithus gracilis
Cryptalithus cabbaldi
Resserella paracyclica
Hedstraemina rabusta
Kjerulfina palycyma
Wattsella unguis
Wattsella wattsi
Heterarthina praeculta
Kjaerina geniculata
Kjaerina bipartita
Onnia superba
Onnia gracilis
Onnia cabbaldi
Onniella grandis
Onniella reuschi
Wattsella unguis
Wattsella wattsi
Kjaerina geniculata
Raymandella gigantea
Kjaerina bipartita
Onny Shales
Actan Scott Beds
Langville Flags
Upper
Middle
Lawer

Fig. 11 Previous zonal and stratigraphic schemes of Bancroft, 1928–49.

dominated by *Broeggerolithus longiceps*. The fauna is not diverse nor abundant and is mainly limited to shell beds. The upper half of the Glynboro Member contains a complex of new species. The most abundant species are the brachiopods *Kjaerina typa* and *Dalmanella multiplicata multiplicata*. *S. sericea* occurs in small numbers as well as *Paracraniops doyleae*. One of the most characteristic brachiopods of this unit is *Dolerorthis virgata*. It is never abundant but persistently present. An important local extinction is that of *Bancroftina typa*. Trilobites continue from below with little change, dominated by *B. longiceps*, but *Chasmops extensus* becomes more abundant. Other important faunal aspects include the increase in abundance of *Tentaculites anglicus* and the introduction of a few bivalves, notably '*Avicula*' *orbicularis*. The fauna of the upper part of the Glynboro Member is more diverse than the lower part.

The Crosspipes Member is only some 60 m thick, but three distinct faunal developments are seen. These correspond to the three original brachiopod zones, *Wattsella wattsi*, *Wattsella unguis* and *Onniella reuschi*, which Bancroft (1933) erected. The lowest fauna (*c*. 25 m of strata) consists of some species from the uppermost Glynboro Member but with important new elements. *Tentaculities anglicus* tends to dominate the fauna. As a group the brachiopods are still most abundant, such strophomenides as *Kjerulfina trigonalis* and *Strophomena grandis* being characteristic. Both of these are new to the area and they are never common, although persistent. The dalmanellid *Bancroftina hewitti* (reintroduction of the genus *Bancroftina*) and the heterorthiid *Heterorthina praeculta* are restricted to this faunal unit and, with abundant *Dalmanella multiplicata multiplicata*, characterize the whole assemblage. *Sowerbyella sericea* is more abundant than in the preceding assemblage. The most striking absentee from this unit is the *Kjaerina* species group, which does not reappear in the Caradoc succession. The top 3 m of this assemblage

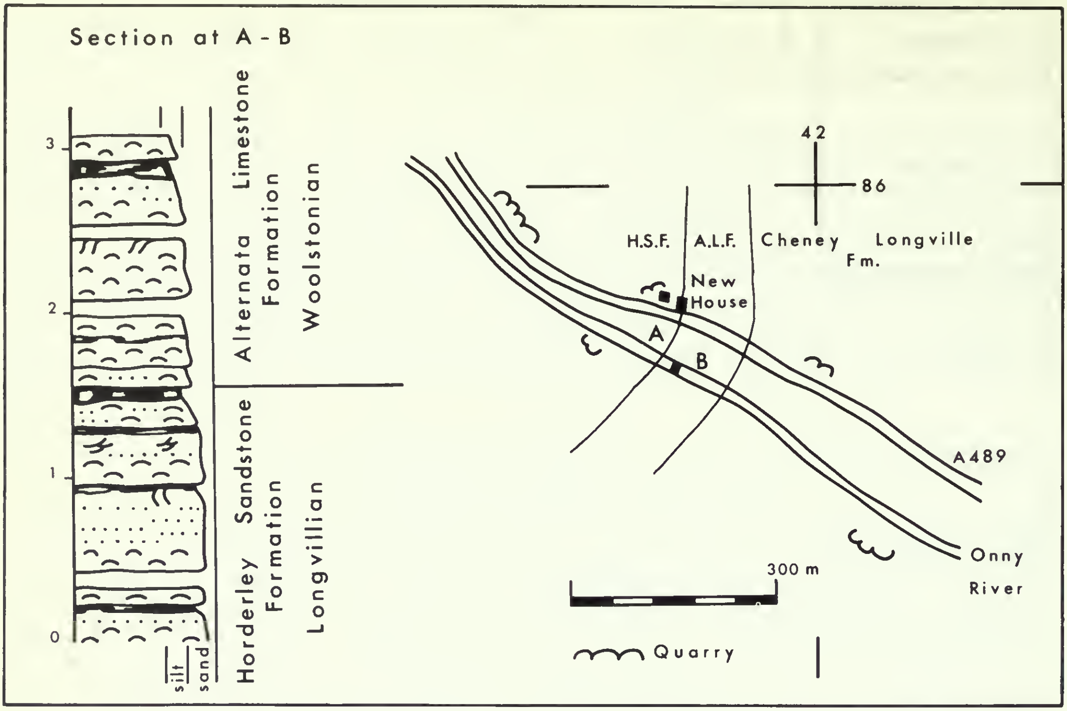


Fig. 12 Location and stratotype section for (1) the boundary between the Horderley Sandstone Formation and the Alternata Limestone Formation, and (2) the Longvillian and Woolstonian Stages. Symbols explained in Fig. 4.

is characterized by the abrupt disappearance of *D. multiplicata multiplicata* and its replacement by *Dalmanella wattsi*. *Heterorthina praeculta* is more abundant in this interval, which Bancroft originally termed the *H. praeculta* superzone.

Of the non-brachiopods a prasoporid bryozoan becomes common. The only new trilobite which is common and diagnostic of this assemblage is *Broeggerolithus transiens*. Other trilobites are similar to the preceding faunal assemblages, although *Brongniartella bisulcata* is uncommon but persistent, whereas *Chasmops extensus* and *Flexicalymene caractaci* increase in numbers. Bivalves are uncommon, but include small individuals of *Similodonta* sp. and *Nuculites planulatus*.

This assemblage is abruptly replaced by one dominated by *Dalmanella unguis* and *Tentaculites anglicus*; the latter reaches its acme in this fauna. Rarer but diagnostic species include *Strophomena grandis* and *Kjerulfina trigonalis* which persist from the basal assemblage, but become more abundant. This assemblage marks the first appearance of *Hedstroemina*, here *H. fragilis*, which is rare. Apart from *S. sericea* which is also rare, the remaining fauna is similar to the preceding assemblage. In the upper half of this subunit the total fauna becomes rarer and the brachiopod individuals, of every species, become smaller. Such changes presumably relate to a local ecological event.

The upper faunal assemblage (*c*. 10 m) is distinguished by both species introductions and local extinctions. *Tentaculites anglicus* becomes rare (Hurst & Hewitt 1977) as does *D. unguis*. Other reductions include *S. grandis*, whilst *K. trigonalis* is totally lost. A characteristic feature of the assemblage is the sudden introduction and dominance of *Onniella reuschi*. This is accompanied by the reintroduction of common *S. sericea*, a large increase in abundance of *H. fragilis*, often dominating single horizons, and the appearance of *K. polycyma*. Other introductions include *Rhactorthis grandis*, *Reuschella bilobata* (in abundance), *Horderleyella* cf. *plicata* and *Leptaena salopiensis*. Bryozoans increase in abundance and diversity as prasoporid, ramose and stick morphotypes become common. Bivalves are commonly represented by *Similodonta* sp. with less

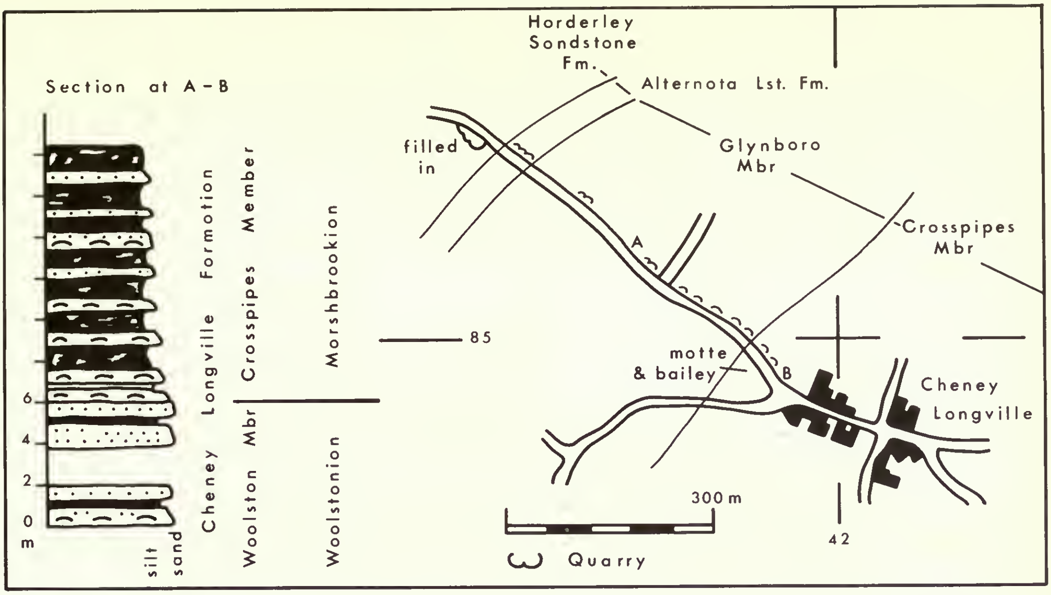


Fig. 13 Location and stratotype section for (1) the boundary between the Glynboro Member and Crosspipes Member of the Cheney Longville Formation, and (2) the Woolstonian and Marshbrookian Stages. Symbols explained in Fig. 4.

common '*Avicula*' *orbicularis* and *Nuculites planulatus*. Gastropods are not common and are often indeterminable, although apparently chiefly bellerophontaceans. The trilobite fauna appears similar in species composition to the underlying assemblage, but changes in abundance occur. *B. transiens* and *C. extensus* are rarer; the most common form is *Flexicalymene caractaci*. *Primaspis caractaci* makes its first appearance. The upper assemblage is very diverse, with a more abundant fauna (high density) than the preceding faunal units. This assemblage also marks the initial shift in abundance changes for major taxa, for instance the bivalves and gastropods are numerically important for the first time; this trend continues into the units above (Hurst & Hewitt 1977).

Based on faunal differences, Dean (1958) subdivided the Acton Scott Formation of the Onny Valley into three. Here only a bipartite faunal division is recognized; the faunal assemblages correlating with the two member units of the formation. The lowest faunal assemblage, in the Ragdon Member, does not differ greatly in diversity and density from the preceding unit, and represents only a change in faunal emphasis. *Onniella reuschi* is still dominant, with other common forms such as *H. fragilis*, *L. salopiensis*, *Rhactorthis* cf. *crassa* and *R. bilobata*. *Kjerulfina polycyma* disappears but a few rare species like *Zygospira* sp., *Skenidioides* cf. *costatus* and *Obolus salopiensis* appear. *Cryptothyris paracyclica* and *Nicolella actoniae*, which become more abundant later, make their first tentative appearance. The most important brachiopod introduction is *Chonetoidea radiatula* which is abundant and diagnostic.

Trilobites are not common, but include *Flexicalymene laticeps*, *Primaspis caractaci* and *Calyptaulax actonensis*. The most important feature of this faunal unit is the increase in molluscan numbers. Bivalves, especially *Similodonta* sp., are common and include *Nuculites planulatus*, *Praeleda* sp., *Cuneamya* cf. *miamiensis* and *Modiolopsis* spp. A and B, many occurring for the first time. Gastropods are represented by *Kokenospira* sp., *Temnodiscus* sp., *Liospira* sp., *Cymbularia* sp. and *Carinaropsis* sp. and are never abundant but always persistent. The monoplacophoran *Archinacella* sp. makes its first appearance, as do the rare orthocones '*Orthoceras*' cf. *subundulatum*, '*O.*' *pictum*, *Poterioceras* sp. and *Cyrtoceras* sp.

The uppermost faunal assemblage of the Acton Scott Formation of the Onny Valley is very distinct from the preceding unit. Not only is the total fauna less diverse and with a lower density, but there is also a significant species turnover event. The unit as a whole is characterized by

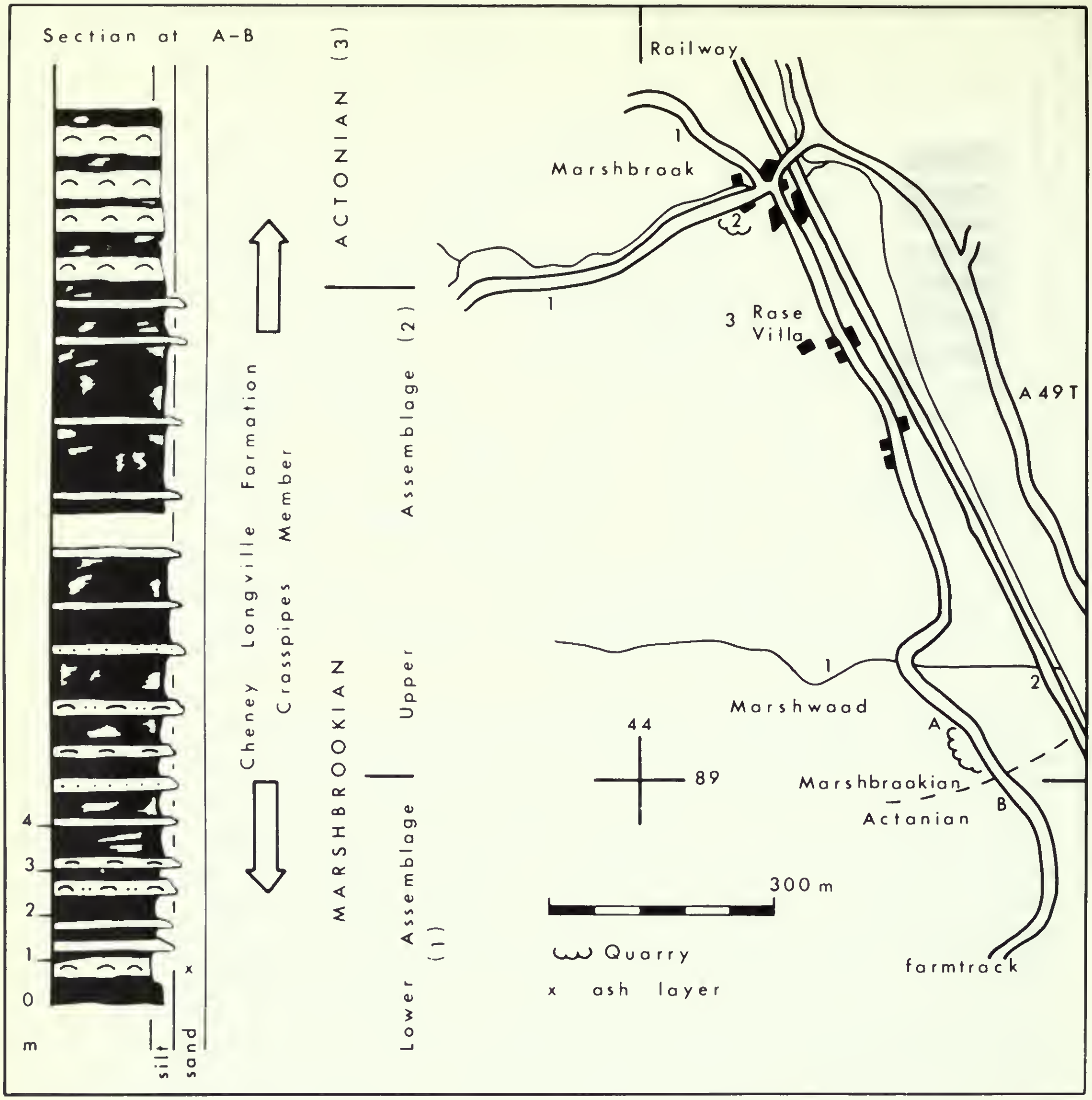

Section at A–B
ACTONIAN (3)
Cheney Longville Formation
Crosspipes Member
MARSHBROOKIAN
Upper Assemblage (2)
Lower Assemblage (1)
4
3
2
1
0
m
x
silt
sand
Railway
1
Marshbrook
2
1
3 Rose Villa
A 49 T
1
2
Marshwood
44
89
A
B
Marshbrookian
Actonian
300 m
Quarry
x ash layer
farmtrack

Fig. 14 Location and stratotype section for the boundary between the Marshbrookian and Actonian Stages. Symbols explained in Fig. 4.

diversity of tribolites such as *Ampyxella edgelli*, *Tretaspis ceriodes favus*, *Calyptaulax actonensis*, *Lonchodomas pennatus*, *Flexicalymene laticeps*, *Platylichas laxatus*, *Illaenus* (*Parillaenus*) cf. *fallax* and *Remopleurides latus onniensis*. However, the most abundant species are still brachiopods, particularly *Onniella depressa* (which replaces *O. reuschi*) and *Cryptothyris paracyclica*. *Eoplectodonta* cf. *rhombica* occurs persistently and for the first time, but is never common. Bryozoans are rare and limited to a single ramose form. Bivalves are still represented mainly by *Similodonta* sp. and subordinate *Nuculites planulatus*, but gastropods are rarer, chiefly *Kokenospira* and also *Lytospira* sp. and *Clathrospira* sp.

In the Acton Scott area there is a local variation in this assemblage. *Nicolella actoniae* is locally abundant in some limestone bands and *Cryptothyris paracyclica* is consistently more abundant than *Onniella depressa*. *Leptestiina oepiki* is more common and *Eoplectodonta* cf. *rhombica* is

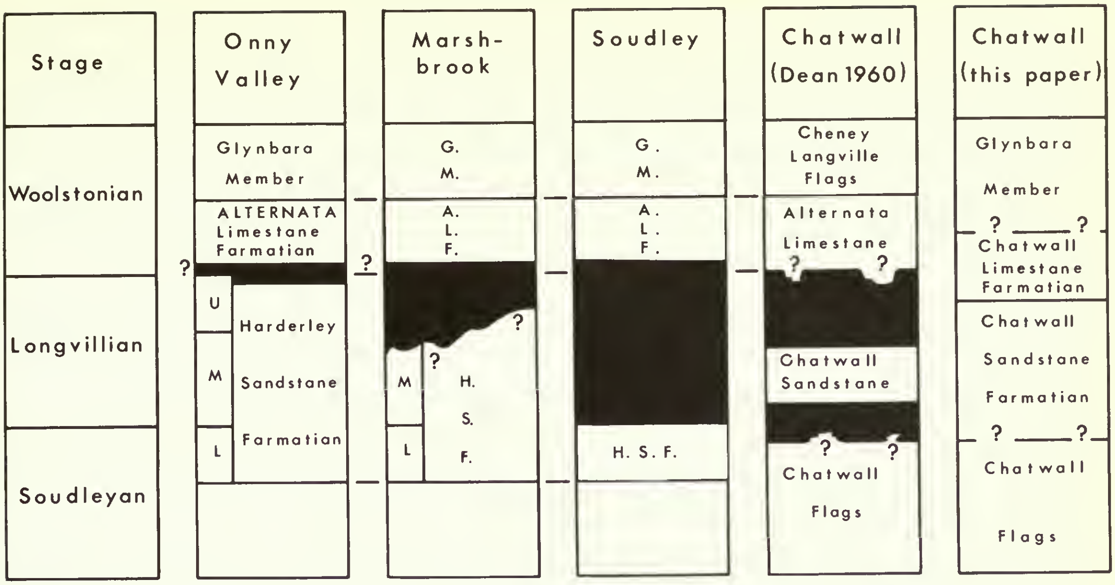

Stage
Woolstonian
Longvillian
Soudleyan
Onny Valley
Glynbara Member
ALTERNATA Limestone Formation
U
M
L
Harderley Sandstone Formation
?
Marshbrook
G. M.
A. L. F.
?
M
L
H. S. F.
Soudley
G. M.
A. L. F.
H. S. F.
Chatwall (Dean 1960)
Cheney Longville Flags
Alternata Limestone
Chatwall Sandstone
Chatwall Flags
Chatwall (this paper)
Glynbara Member
Chatwall Limestone Formation
Chatwall Sandstone Formation
Chatwall Flags

Fig. 15 Correlation problems and possibilities at the base of the Alternata Limestone Formation and between the middle Caradoc strata of the Soudley – Onny Valley and Chatwall districts.

absent. These changes correlate with a change in sediment grain size from calcareous silty muds to calcareous sandy silts.

The Onny Shale Formation has been divided into three successive trilobite zones (Bancroft 1929*b*): *Onnia cobboldi*, *O. gracilis* and *O. superba*. Two assemblages are recognized here, one which corresponds to the two lower zones and one to the upper zone.

The basal faunal assemblage is not diverse but abundant and characterized by large numbers of well-preserved *Onnia*. Other trilobites include *Calyptaulax actoniensis*, *Chasmops extensus*, *Illaenus* (*Parillaenus*) cf. *fallax*, *Lonchodomas pennatus*, *Flexicalymene onniensis*, *Platylichas laxatus*, *Remopleurella burmeisteri* and *Tretaspis ceriodes favus*. Many of these occur in the preceding assemblage, but the rare *C. actoniensis*, *C. extensus* and *P. laxatus* only occur in the lower part of the assemblage. Brachiopods are abundant but not diverse. There is a sudden introduction of large *Onniella broeggeri* (which replaces *O. depressa*) and also *Sericoidea homolensis*, both of which may dominate horizons. Other brachiopods are rare, but include the first occurrence of *Christiania hollii*. Harper (1978) has recorded a rare assemblage with *Heterorthis alternata*, *Onniella* and *Sowerbyella*. Bivalves are not diverse but they are often abundant and are dominated by palaeotaxodonts such as *Nuculites planulatus*, with subordinate *Palaeonucula* sp., *Modiolopsis* sp. B and *Similodonta* sp. Gastropods, though rare, commonly include *Cymbularia* sp., *Sinuites* sp., *Lytospira* sp. and *Temnodiscus* sp.

The uppermost assemblage of the Onny Shale is characterized by its depauperate fauna. Very small *Onniella* sp. (*O. broeggeri* ?) and *Sericoidea* sp. (*S. homolensis* ?) occur, but specific identification is impossible because they are so immature (*c.* 2 mm wide). However, *Christiania hollii* increases in abundance from the underlying faunal assemblage, and *Schizocrania hewardi* appears; both are small forms. The trilobites are reduced in numbers, the most common being *Onnia superba*, but also *Triarthrus* cf. *linnarssoni*, *Pseudosphaeroxochus* sp. and *Eobronteus* sp. *Ampyxella edgelli*, *Lonchodomas pennatus* and *Remopleurella burmeisteri* carry over from the preceding assemblage but are very rare.

Harper (1978) has described a thin discontinuous layer of *Heterorthis alternata* in a fine sandstone matrix of the distal bioturbated muds in the uppermost beds of the type Onnian. Other notable faunal elements include *Onniella* and *Sowerbyella*. It is probable that at least *H. alternata* and *Sowerbyella* were introduced by the distal effects of a storm pulse from a near-shore environment (Hurst 1979). As the *Onniella* was not specifically determined it is not known whether it was significantly transported (cf. Hurst 1978). This find demonstrates that *H. alternata* is not a good stratigraphic indicator for the Woolstonian. But this unusual occurrence may have palaeogeographic implications; *H. alternata* is common in near-shore environments and its presence in the Onnian suggests their encroachment and may possible indicate the persistence of the feature responsible for the Henley Member into Onnian times. Alternatively, the Henley Member may be a correlative of the Onnian Onny Shale Formation.

Outside the Onny Valley, the Henley Member contains a mixture of faunas but it is difficult to assess their spatial and temporal ranges, owing to the poor exposures, but in the quarry at SO 449896 two faunal assemblages occur (Fig. 9). The lower one is a low diversity and density assemblage dominated by abundant, but small, *Dalmanella unguis ultima*, less common *Strophomena grandis* and rare *Hedstroemina fragilis*, *Reuschella bilobata* and *Leptestiina* sp. The most abundant species is *Tentaculites anglicus*, whilst a prasoporid bryozoan is also common, as is the trilobite *Broeggerolithus transiens*, but only two other rare species have been recorded, *Primaspis caractaci* and *Gravicalymene* cf. *praecox*. This assemblage is similar in species content to the middle faunal unit of the Crosspipes Member.

Above comes a more diverse and altogether richer faunal assemblage (Fig. 9) dominated by *Onniella reuschi* and *Sowerbyella sericea*. *Hedstroemina fragilis* and *Kjerulfina polycyma* are also abundant in certain beds. Other diagnostic but less common species include *Rhactorthis actoniae*, *Leptaena salopiensis* and *Obolus* sp. *Tentaculites anglicus* is rare, whilst bryozoan diversity increases to include ramose, stick and prasoporid morphotypes. The tribolite fauna is not diverse nor common and only two species, *Broeggerolithus transiens* and *Gravicalymene* cf. *praecox*, have been found. This assemblage also parallels the uppermost faunal unit of the Crosspipes Member.

The small isolated rock garden exposure at Acton Scott (SO 454893) contains an assemblage unique in the whole of the type upper Caradoc succession, dominated by *Cryptothyris paracyclica* and *Dalmanella unguis ultima* with subordinate *Skenidioides* cf. *costatus*, *Leptestiina* sp., *Paracraniops doyleae*, *Orbiculoidea salopiensis* and *Dolerorthis virgata*. Trilobites are rare and include *Gravicalymene* cf. *praecox*, *Primaspis caractaci* and *Otarion* sp. Ramose bryozoan colonies are common.

The type section for the Chatwall Sandstone and Chatwall Limestone Formations is now conserved and thus no faunal collecting was possible from there. However, the Chatwall Sandstone Formation contains little fauna: Dean (1960*a*) reported rare *Kjaerina* aff. *jonesi*, *Sinuites* sp. and *Lophospira* cf. *gyrogonia* in the lower half, and at the very top *Dalmanella lepta*, *Rostricellula* sp., *Sowerbyella soudleyensis*, *Broeggerolithus* cf. *globiceps*, *Brongniartella* cf. *parva*, ? *Parabasilicus powisii* and *Lophospira* sp. ind. The assemblage from the Chatwall Limestone Formation (see also list in Dean 1960*a*) is similar to that found in the uppermost Horderley Sandstone Formation, Alternata Limestone Formation and overlying lowermost Cheney Longville Formation of the Onny Valley.

Chronostratigraphy: Stage definitions and recognition

When Bancroft (1929*a*, *b*, 1933, 1945) erected the Caradoc Stages he defined them by means of brachiopods and trilobites (see Fig. 3, p. 189) but, although Bancroft gave type areas for the stages, he did not tie the boundaries down in particular sections. This fault is remedied here. All stages are defined within the southern area, between Acton Scott and Cheney Longville, as indicated by Bancroft and where possible in the Onny Valley itself.

a. Woolstonian Stage

Previously termed the Upper Longvillian Substage, the new name (after the village of Woolston, SO 424872, two miles north of the Onny Valley) is introduced for several reasons. The original concept of a Longvillian Stage (Bancroft 1929*a*) encompasses a great deal of strata within which there is a bipartite faunal division. In the type area the Upper Substage (= Woolstonian) is characterized by a sudden influx of *Heterorthis alternata*, *Trematis punctata*, *Broeggerolithus longiceps* and *Brongniartella bisulcata*. Bancroft (1929*a*) stated that the Longvillian Stage was characterized by the genus *Kjaerina* throughout. This is so, but Woolstonian *Kjaerina* (and *Bancroftina*) are distinguishable from Longvillian forms by their greater size. These faunal differences, as well as the condensed sequence at the base of the Woolstonian in the type area (Onny Valley region), warrant the introduction of this new stage. The Longvillian is retained for the former Lower Longvillian Substage, which includes part of the Horderley Sandstone Formation, in accord with the original definition of Bancroft (1929*a*), who placed both the Horderley Sandstone and Lower Longville Flags in the Longvillian.

Table. Complete faunal list of upper Caradoc species. ALF = Alternata Limestone Formation, CLF = Cheney Longville Formation, GM = Glynboro Member, CM = Crosspipes Member, ASF = Acton Scott Formation, RM = Ragdon Member, WM = Wistanstow Member, OSF = Onny Shale Formation. 1–3 refer to respective faunal assemblages. R = Rare (0–5% of total benthic fauna), P = Present (5–20%), C = Common (20–50%), VC = Very common (+50%). The stratigraphy and so also the faunal list are based solely on the Onny Valley section; the Henley Member of the Acton Scott Formation is thus omitted from the scheme.

	ALF	CLF					ASF		OSF	
		GM		CM			RM	WM		
		1	2	1	2	3			1	2
ANNELIDA										
Onnioides laevis (M'Coy, 1851)	–	–	–	–	–	–	R	R	R	–
scolecodonts	–	–	–	–	–	–	–	R	R	–
Tentaculites anglicus Salter, 1859	R	P	P	C	VC	R	–	–	–	–
BRACHIOPODA										
Bancroftina typa (Whittington, 1938)	P	C	–	–	–	–	–	–	–	–
Bancroftina hewitti sp. nov. (p. 250)	–	–	–	R	–	–	–	–	–	–
Bicuspina sp.	–	–	–	–	–	–	R	R	–	–
Chonetoidea radiatula (Barrande, 1879)	–	–	–	–	R	R	P	P	–	–
Christiania hollii (Davidson, 1871)	–	–	–	–	–	–	–	–	R	R
Cryptothyris paracyclica (Bancroft, 1928)	–	–	–	–	–	–	R	R	–	–
Dalmanella multiplicata prima subsp. nov. (p. 244)	R	R	–	–	–	–	–	–	–	–
Dalmanella multiplicata multiplicata (Bancroft, 1928)	–	–	C	C	–	–	–	–	–	–
Dalmanella unguis unguis (J. de C. Sowerby, 1839)	–	–	–	–	C	–	–	–	–	–
Dalmanella unguis ultima subsp. nov. (p. 246)	–	–	–	–	R	R	R	–	–	–
Dalmanella wattsi (Bancroft, 1928)	–	–	–	C	–	–	–	–	–	–
Destombesium sp.	–	–	–	–	–	R	–	–	–	–
Dinorthis sp.	–	R	R	R	R	R	–	–	–	–
Dolerorthis virgata (J. de C. Sowerby, 1839)	R	R	R	R	R	R	–	R	–	–
Drabovia sp.	–	–	–	–	–	–	R	–	–	–
Elliptoglossa sp.	–	–	–	–	–	–	R	–	–	–
Eoplectodonta cf. *rhombica* (M'Coy, 1852)	–	–	–	–	–	–	–	P	R	–
Hedstroemina fragilis Bancroft, 1929	–	–	–	–	R	P	P	–	–	–
Heterorthina praeculta Bancroft, 1928	–	–	–	R	–	–	–	–	–	–
Heterorthis alternata (J. de C. Sowerby, 1839)	VC	R	–	–	–	R	R	–	–	–
Horderleyella cf. *plicata* Bancroft, 1928	–	–	–	–	–	R	–	–	–	–
Kjaerina bipartita (Salter, 1854)	P	C	–	–	–	–	–	–	–	–
Kjaerina typa Bancroft, 1929	–	–	C	–	–	–	–	–	–	–
Kjerulfina polycyma Bancroft, 1929	–	–	–	–	–	R	–	–	–	–
Kjerulfina trigonalis Bancroft, 1929	–	–	–	R	R	–	–	–	–	–
Leptaena salopiensis Williams, 1963	–	–	–	–	–	–	R	R	–	–
Lingulella sp.	–	–	–	–	–	–	–	–	R	R
Lingulops sp.	–	–	–	–	R	–	–	–	–	–
Marionites typus (Bancroft, 1928)	R	–	–	–	–	–	–	–	–	–

Table (*cont.*)

	ALF	CLF					ASF		OSF	
		GM		CM			RM	WM		
		1	2	1	2	3			1	2
Nicolella actoniae (J. de C. Sowerby, 1839)	–	–	–	–	–	–	R	R	–	–
Obolus salopiensis sp. nov. (p. 223)	–	–	–	–	–	–	R	R	R	–
Onniella broeggeri Bancroft, 1928	–	–	–	–	–	–	–	–	C	P
Onniella depressa Bancroft, 1945	–	–	–	–	–	–	–	C	–	–
Onniella reuschi Bancroft, 1928	–	–	–	–	–	VC	C	–	–	–
Orbiculoidea ovata sp. nov. (p. 230)	–	–	–	–	–	–	R	–	–	–
Orbiculoidea sp.	–	–	–	–	–	–	–	R	–	–
Palaeoglossa lockleyi sp. nov. (p. 225)	–	–	–	R	R	R	R	–	–	–
Paracraniops doyleae sp. nov. (p. 227)	R	R	R	R	R	R	R	–	–	–
Paterula cf. *subcircularis* Cooper, 1956	–	–	–	–	–	–	–	–	R	–
Paterula sp.	–	–	–	–	–	–	R	–	–	–
Platystrophia sp. 1	–	–	–	–	R	–	–	–	–	–
Platystrophia sp. 2	–	–	–	–	–	–	R	–	–	–
Plectorthid gen. et sp. indet.	–	–	–	–	–	–	R	–	–	–
Pseudolingula sp.	–	–	–	–	–	R	R	–	–	–
Reuschella bilobata (J. de C. Sowerby, 1839)	R	R	R	R	R	R	R	R	–	–
Rhactorthis cf. *crassa* Williams, 1963	–	–	–	–	–	–	R	–	–	–
Rhactorthis grandis sp. nov. (p. 239)	–	–	–	–	–	R	–	–	–	–
Schizocrania hewardi sp. nov. (p. 229)	–	–	–	–	–	–	–	–	–	C
Schizocrania salopiensis Williams, 1974	–	–	–	–	R	R	R	–	–	–
Schizotreta sp. 1	–	–	–	–	–	–	–	–	–	R
Schizotreta sp. 2	–	–	–	–	–	–	R	–	–	–
Sericoidea homolensis Havlíček, 1967	–	–	–	–	–	–	–	–	C	C
Skenidioides cf. *costatus* Cooper, 1956	–	–	–	–	–	–	R	–	–	–
Sowerbyella sericea (J. de C. Sowerby, 1839)	VC	P	R	C	R	C	R	–	–	–
Strophomena grandis (J. de C. Sowerby, 1839)	–	–	–	R	R	–	–	–	–	–
Trematis punctata (J. de C. Sowerby, 1839)	R	–	–	–	–	–	–	–	–	–
Triplesia sp.	–	–	–	–	–	–	R	–	–	–
? *Zygospira* sp.	–	–	–	–	–	–	R	–	–	–
BRYOZOA										
prasoporid morphotype	R	R	R	P	R	R	R	–	–	–
ramose morphotype	R	R	R	R	R	R	R	–	–	–
stick morphotype	R	R	R	R	R	R	R	–	–	–
BIVALVIA										
? *Ambonychia radiata* Hall, 1847	–	R	R	–	–	–	–	–	–	–
? *Avicula orbicularis* Hall, 1843	R	R	R	R	R	R	R	R	–	–
Cuneamya cf. *miamiensis* Hall & Whitfield, 1875	–	–	–	–	–	–	R	–	–	–
Cyclochoncha sp.	–	–	–	–	–	–	R	–	–	–
? cyclochonchid	–	–	–	–	–	–	R	–	–	–
? *Modiolodon* sp.	R	–	–	–	–	–	–	–	–	–
Modiolopsis sp. A	–	–	–	R	R	R	R	R	–	–
Modiolopsis sp. B	–	–	–	–	–	–	R	R	–	–
Modiolopsis sp.	–	–	–	–	–	–	R	–	–	–
Modiolopsis cf. *modiolaris* (Conrad, 1838)	R	R	R	–	–	–	–	–	–	–
Modiolopsidae	–	–	–	R	R	R	–	–	–	–
Nuculites planulatus Conrad, 1841	–	–	–	R	R	R	R	P	R	R
? *Nuculites* sp.	–	–	–	–	–	–	–	–	R	–
Palaeoneilo sp.	–	–	–	R	R	R	R	–	–	–
Palaeonucula sp.	–	–	–	–	–	–	R	R	R	–

Table (*cont.*)

	ALF	CLF					ASF		OSF	
		GM		CM			RM	WM		
		1	2	1	2	3			1	2
? *Praearca* sp.	–	–	–	–	–	–	R	R	–	–
? *Praeleda* sp.	–	–	–	–	–	–	R	R	–	–
Similodonta sp.	–	R	R	R	R	R	P	P	R	R
undetermined bivalves	R	R	R	R	R	R	R	R	R	R
CEPHALOPODA										
'*Cyrtoceras*' sp.	–	–	–	–	R	–	–	–	–	–
'*Orthoceras*' *pictum* Blake, 1882	–	–	–	–	–	–	R	R	–	–
'*Orthoceras*' cf. *subundulatum* Portlock, 1843	–	–	–	–	–	–	R	R	–	–
'*Poterioceras*' sp.	–	–	–	–	–	–	R	–	–	–
GASTROPODA										
? *Arjamannia* sp.	–	–	–	–	–	–	–	R	–	–
Carinaropsis sp.	–	–	–	–	–	–	R	–	–	–
Clathrospira sp.	–	–	–	–	–	–	–	R	–	–
Cymbularia sp.	–	–	–	–	–	–	R	R	R	–
Kokenospira sp.	–	–	–	–	–	–	R	R	–	–
Liospira sp.	–	–	–	–	–	–	R	R	–	–
Lophospira sp.	–	–	–	–	R	R	–	–	–	–
Lytospira sp.	–	–	–	–	–	–	–	R	R	–
Phragmolites sp.	–	–	–	–	R	–	–	–	–	–
Sinuites sp.	–	–	–	–	–	R	R	R	R	–
Temnodiscus sp.	–	–	–	–	–	–	R	R	R	–
Trochonema sp.	–	–	–	–	R	–	–	–	–	–
indeterminate bellerophontaceans	–	–	–	–	–	–	R	R	R	–
indeterminate gastropod sp. 1	–	–	–	–	–	–	–	R	–	–
indeterminate gastropod sp. 2	–	–	–	–	–	–	–	R	–	–
indeterminate gastropods	R	R	R	R	R	R	R	R	R	–
indeterminate pleurotomariaceans	–	–	–	–	–	–	R	R	–	–
indeterminate trochiforms	R	–	–	–	–	–	R	–	–	–
MONOPLACOPHORA										
Archinacella sp.	–	–	–	–	–	–	R	R	–	–
Cyrtolites sp.	–	–	–	–	–	–	–	–	R	–
indeterminate monoplacophorans	–	–	–	–	–	–	R	R	R	–
OSTRACODA										
Tallinnella scripta (Harper, 1947)	R	R	R	R	R	R	R	–	–	–
Primitia sp.	–	–	–	–	–	R	R	R	R	R
TRILOBITA										
Ampyxella edgelli (Reed, 1910)	–	–	–	–	–	–	–	R	R	R
Broeggerolithus longiceps (Bancroft, 1929)	R	R	R	–	–	–	–	–	–	–
Broeggerolithus transiens (Bancroft, 1929)	–	–	–	R	R	R	–	–	–	–
Brongniartella bisulcata (M'Coy, 1851)	R	R	R	R	R	R	–	–	–	–
Calyptaulax actonensis Dean, 1961	–	–	–	–	–	–	R	R	R	–
Chasmops extensus (Boeck, 1837)	R	R	R	R	R	R	R	R	R	–
Decoroproetus sp.	–	–	–	–	R	–	–	–	–	–
Encrinurus sp.	–	–	–	–	R	–	–	–	–	–
? *Eobronteus* sp.	–	–	–	–	–	–	–	–	–	R
Flexicalymene caractaci (Salter, 1865)	–	–	–	R	R	R	–	–	–	–

Table (*cont.*)

	ALF	CLF					ASF		OSF	
		GM		CM			RM	WM		
		1	2	1	2	3			1	2
Flexicalymene cobboldi Dean, 1962	R	R	R	–	–	–	–	–	–	–
Flexicalymene laticeps (Bancroft, 1949)	–	–	–	–	–	–	R	R	–	–
Flexicalymene onniensis (Shirley, 1936)	–	–	–	–	–	–	–	–	R	R
Flexicalymene salteri (Bancroft, 1949)	–	–	–	–	–	–	–	R	–	–
Gravicalymene inflata Dean, 1962	–	–	–	–	–	–	–	–	R	–
Gravicalymene cf. *praecox* (Bancroft, 1949)	–	–	–	–	–	–	–	–	R	–
Illaenus cf. *fallax* Holm, 1882	–	–	–	–	–	–	–	–	R	–
Illaenus sp.	–	–	–	–	–	–	–	R	R	–
Kloucekia (*Phacopidina*) *apiculata* (M'Coy, 1851)	R	R	R	–	–	–	–	–	–	–
Lonchodomas pennatus (La Touche, 1884)	–	–	–	–	–	–	–	R	R	R
Onnia cobboldi (Bancroft, 1929)	–	–	–	–	–	–	–	–	P	–
Onnia gracilis (Bancroft, 1929)	–	–	–	–	–	–	–	–	C	–
Onnia superba (Bancroft, 1929)	–	–	–	–	–	–	–	–	–	C
Otarion sp.	–	–	–	R	R	R	–	–	–	–
Platylichas laxatus (M'Coy, 1846)	–	–	–	–	–	–	–	R	R	–
Primaspis caractaci (Salter, 1853)	–	–	–	–	–	R	R	–	–	–
Pseudosphaerexochus sp.	–	–	–	–	–	–	–	–	–	R
Remopleurella burmeisteri (Bancroft, 1949)	–	–	–	–	–	–	–	–	R	R
Remopleurides latus onniensis Dean, 1962	–	–	–	–	–	–	–	R	–	–
Tretaspis ceriodes favus Dean, 1963	–	–	–	–	–	–	–	R	R	–
Triarthrus cf. *linnarssoni* Thorslund, 1940	–	–	–	–	–	–	–	–	–	R
MISCELLANEA										
Hyolithes sp.	–	–	–	–	–	–	–	–	–	R
solitary corals	–	–	–	–	–	–	–	R	R	–
crinoid ossicles	R	R	R	R	R	R	R	–	–	–
phyllocariids	–	–	–	–	–	–	–	–	R	R

The junction between the Horderley Sandstone Formation and Alternata Limestone Formation is seen in the bed of the Onny River (SO 418856). This is the standard section for the base of the Woolstonian Stage and is shown in Fig. 12. The base of the Woolstonian coincides with the base of the Alternata Limestone Formation. The topmost collection from the Horderley Sandstone Formation (Hurst 1979) contained small *Kjaerina bipartita* (61%), *Sowerbyella sericea* (21%), small *Bancroftina typa* (4%), *Brongniartella minor* (2%), ramose bryozoan (2%), prasoporid bryozoan (10%) and rare round crinoid ossicles. The lowermost Alternata Limestone Formation collection contained large *Bancroftina typa* (53%), *Sowerbyella sericea* (23%), *Heterorthis alternata* (15%), *Trematis punctata* (7%), *Brongniartella bisulcata* (2%) and fragments of gastropods. Some 5 cm above this collection the fauna contained in a single bed included *Trematis punctata* (11%), large *Bancroftina typa* (13%), *Heterorthis alternata* (65%), large *Kjaerina bipartita* (5%), *Sowerbyella sericea* (1%), *Broeggerolithus longiceps* (2%), *Modiolopsis* cf. *modiolaris* (2%) and an indeterminate trochinid gastropod (1%). The sudden influx of *H. alternata* and *T. punctata* marks the base of the Woolstonian.

Bancroft (1945 : 183) stated that the type section for the Upper Longvillian was 'in the Longville Flags of Longville Lane, from the base of the *Alternata* Limestone to the Earthwork'. Most of the lower part of this section is now overgrown, but the upper part is exposed and includes the type section for the Woolstonian/Marshbrookian boundary.

The junction between the Glynboro Member and the Crosspipes Member of the Cheney Longville Formation is seen in the roadside at SO 418851, and that section forms the standard for the

Woolstonian/Marshbrookian boundary (Fig. 13). The uppermost single bed collection in the Woolstonian contains *Dalmanella multiplicata multiplicata* (40%), *Kjaerina typa* (18%), *Tentaculites anglicus* (20%), *Paracraniops doyleae* (2%), *Broeggerolithus longiceps* (2%), *Flexicalymene caractaci* (2%), prasoporid bryozoan (6%), ramose bryozoan (10%) and round crinoid ossicles. Some 110 cm of strata follows in which a non-diagnostic fauna occurs (Fig. 13). This includes *Dalmanella multiplicata multiplicata* (37%), *Bancroftina hewitti* (7%), *Kjaerina typa* (3%), *Tentaculites anglicus* (23%), *Paracraniops doyleae* (13%), *Broeggerolithus longiceps* (3%), *Brongniartella bisulcata* (3%), prasoporid bryozoans (7%) and ramose bryozoans (3%). Some 30 cm above the last collection a diagnostic lower faunal assemblage of the Marshbrookian appears, containing *Dalmanella multiplicata multiplicata* (33%), *Bancroftina hewitti* (1%), *Kjerulfina trigonalis* (2%), *Strophomena grandis* (2%), *Sowerbyella sericea* (15%), *Broeggerolithus transiens* (1%), *Flexicalymene caractaci* (1%), *Brongniartella bisulcata* (1%), *Tentaculites anglicus* (16%), prasoporid bryozoan (26%), ramose bryozoans (1%), smooth and ribbed ostracods, and round and pentagonal crinoid ossicles. The loss of *K. typa* and the introduction of a more diverse fauna with *S. sericea*, *K. trigonalis*, *S. grandis*, *B. hewitti* and *B. transiens* marks the boundary between the two stages.

b. Marshbrookian Stage

Bancroft (1945 : 183) stated that the type section for this unit was through 'the highest beds of the Longville Flags as exhibited in the lane through Marsh Wood'. This is still the best section (SO 445890), even though it is now becoming overgrown, but unfortunately the base of the Marshbrookian is not exposed (see Fig. 14). The top of the uppermost faunal assemblage of the Crosspipes Member (*Onniella reuschi* Zone of Bancroft) has always been taken as the boundary between the Marshbrookian and Actonian. However, this boundary is here redefined to coincide with the top of the middle assemblage (*Dalmanella unguis* Zone of Bancroft) of the Crosspipes Member. The stratotype is defined in the cart track just to the south of Marshwood Quarry (Fig. 14).

The Marshbrookian/Actonian boundary is redefined here, because a major faunal turnover and species replacement, with a major change in diversity and density, occur at this point, i.e. between the middle and upper faunal assemblages of the Crosspipes Member of the Cheney Longville Formation. The boundary is traceable throughout the Caradoc district and in fact was partially exposed through trenching in the Onny Valley (SO 422854; see Fig. 8); it is accessible in the stream section at Ragleth Hill (SO 451908 to SO 451906; see Fig. 7). Such redefinition limits the diverse *Onniella* faunas of the Upper Caradoc to post-Marshbrookian strata and the majority of the less diverse *Dalmanella*-dominated faunas to the pre-Actonian.

In the standard section for the boundary (Fig. 15) the uppermost single bed collection from the Marshbrookian contains the following species: *Dalmanella unguis unguis* (20%), *Paracraniops doyleae* (7%), *Hedstroemina fragilis* (3%), *Sowerbyella sericea* (3%), *Strophomena grandis* (3%), *Chonetoidea radiatula* (1%), *Tentaculites anglicus* (49%), *Broeggerolithus transiens* (2%), *Flexicalymene caractaci* (1%), *Brongniartella bisulcata* (1%), *Decoroproetus* sp. (1%), *Otarion* sp. (1%), prasoporid bryozoans (7%), thin ramose bryozoans (1%), smooth and ribbed ostracods and round and pentagonal crinoid ossicles. Precisely 1 m higher stratigraphically, the lowest collection from the Actonian contains *Onniella reuschi* (59%), *Sowerbyella sericea* (8%), *Hedstroemina fragilis* (5%), *Kjerulfina polycyma* (1%), *Palaeoglossa lockleyi* (0·5%), *Paracraniops doyleae* (0·5%), *Schizocrania salopiensis* (0·5%), *Reuschella bilobata* (1·5%), *Heterorthis alternata* (0·5%), *Rhactorthis grandis* (1%), *Similodonta* sp. (5%), *Modiolopsis* sp. A (3%), '*Avicula*' cf. *orbicularis* (3%), *Nuculites planulatus* (3%), *Flexicalymene caractaci* (1%), *Primaspis caractaci* (0·5%), *Tentaculites anglicus* (4%), prasoporid bryozoans (2%), ramose bryozoans (2%), indeterminate gastropods (1%) and some round crinoid ossicles.

This abrupt faunal change is one of the most prominent in the upper Caradoc sequence and may represent more than just a local ecological event.

c. Actonian Stage

Bancroft (1945 : 183) listed the type locality for the Actonian as 'the Acton Scott Beds below the

Onnia horizon in the Onny River section east of Burrell's Coppice'. This is the only possible locality for a more or less uninterrupted section, albeit largely unexposed, of this stage (Fig. 8). The base of the Actonian as understood here, or indeed as Bancroft defined it, is not exposed (SO 422854), thus the lower boundary is placed at the locality for the type Marshbrookian (Fig. 14).

d. Onnian Stage

The Onnian is defined, following Bancroft, in the Onny Valley river section between SO 425854 and SO 426854. Bancroft defined the base of the stage, and thus the top of the Actonian, by the sudden appearance of the trilobite genus *Onnia*. There is no need to alter this definition of the Actonian–Onnian stratotype, which is only partially exposed at one locality in the river bed, at SO 425854 (Fig. 8). The boundary is recognizable by the introduction of several new genera and species, not just *Onnia*. The highest single bed collection in the Actonian yielded *Onniella depressa* (14%), *Cryptothyris paracyclica* (2%), *Dolerorthis virgata* (2%), *Eoplectodonta* cf. *rhombica* (25%), *Obolus salopiensis* (3%), *Similodonta* sp. (9%), *Nuculites planulatus* (3%), *Palaeonucula* sp. (4%), *Praearca* sp. (9%), ? cyclonchiid (2%), indeterminate bivalves (5%), *Chasmops extensus* (1%), *Lonchodomas pennatus* (1%), *Ampyxella edgelli* (1%), *Remopleurides latus onniensis* (2%), *Flexicalymene laticeps* (1%), *Kokenospira* sp. (8%), *Cymbularia* sp. (2%), indeterminate gastropods (2%), '*Orthoceras*' cf. *subundulatum* (1%), ramose bryozoans (1%), button bryozoans (1%) and smooth ostracods. A gap of 2–3 m intervenes before the lowest single Onnian collection which yielded *Onniella broeggeri* (44%), *Sericoidea homolensis* (20%), *Eoplectodonta* cf. *rhombica* (2%), *Paterula* cf. *subcircularis* (2%), *Onnia cobboldi* (10%), *Lonchodomas pennatus* (3%), *Chasmops extensus* (1%), *Gravicalymene* cf. *praecox* (4%), *Temnodiscus* sp. (2%), '*Orthoceras*' cf. *subundulatum* (1%), *Nuculites planulatus* (9%), *Palaeonucula* sp. (1%) and smooth ostracods.

Correlation problems within the area

The Onny Valley is the only locality where the upper Caradoc formations are exposed in a more or less continuous sequence and uninterrupted by faulting. The sequence is also complete; that is, apart from the possible condensed sequence or non-sequence at the base of the Alternata Limestone Formation, there are no apparent stratigraphic breaks. However, in the Marshbrook to Soudley district there is certainly a non-sequence between the Alternata Limestone Formation and the underlying Horderley Sandstone Formation. Other problems are the correlation of the

Fig. 16 Soudley Quarry, SO 477918, showing the conformable contact (dotted line) between the Horderley Sandstone Formation (HS) and the Alternata Limestone Formation (AL). The whole of the Longvillian Stage is missing at the dotted line. Note that the Horderley Sandstone Formation is laminated sand whilst the Alternata Limestone Formation is an alternation of laminated sand and bioturbated sandy silts. Section height 2 m.

Fig. 17 Glynboro Member of the Cheney Longville Formation at the old river cliff locality in the Onny Valley at SO 422890. Note the alternation of thick laminated sand units (base of major sandstones marked by dotted line) and bioturbated sandy silts. Upper faunal assemblage; knife 25 cm.

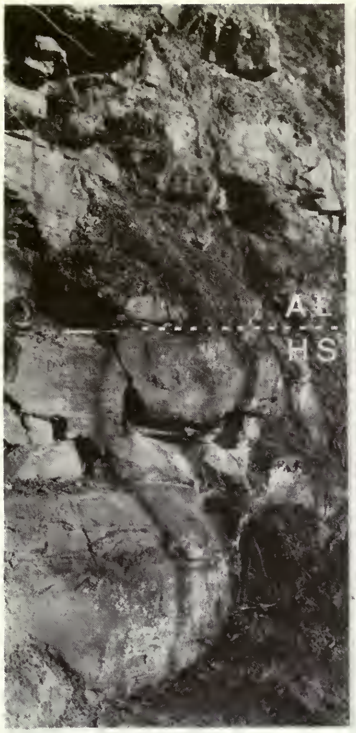
Fig. 18 Swell lag shell layers in completely bioturbated sandy silts of the uppermost part of the Crosspipes Member of the Cheney Longville Formation at the Ragleth Hill stream section at SO 451908. Upper faunal assemblage, × 1, BB 73673.

Fig. 19 A cross-bedded unit in the lower part of the Horderley Sandstone Formation in the Onny Valley at SO 4161 8578.

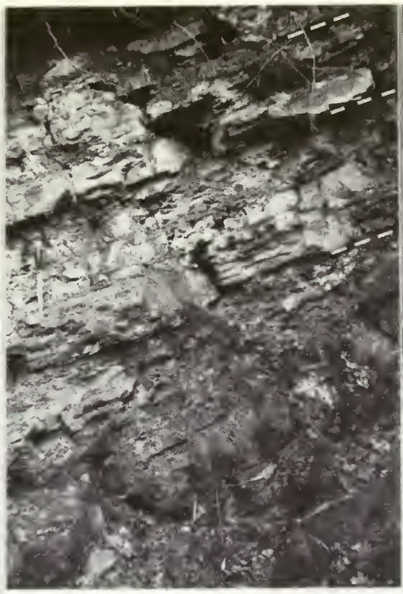
Fig. 20 Close-up of the basal Crosspipes Member of the Cheney Longville Formation at SO 419849. This is the basal faunal assemblage of the Marshbrookian. Note thicker bioturbated horizons than in the Glynboro Member. Knife 25 cm.

Fig. 21 Laminated and low-angled bedding (picked out by dotted shell beds) in the upper part of the Horderley Sandstone Formation in the Onny Valley at SO 4154 8593.

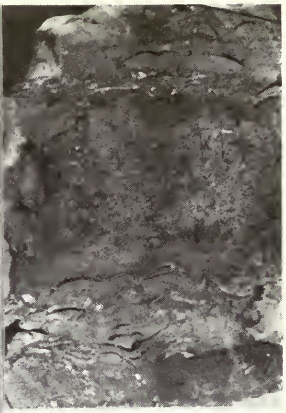
Fig. 22 Close-up of the Alternata Limestone Formation at Soudley Quarry, SO 477918. Knife 25 cm.



16



17



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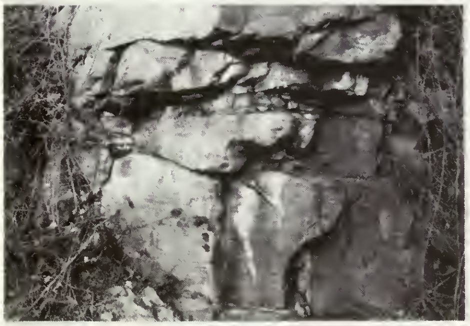

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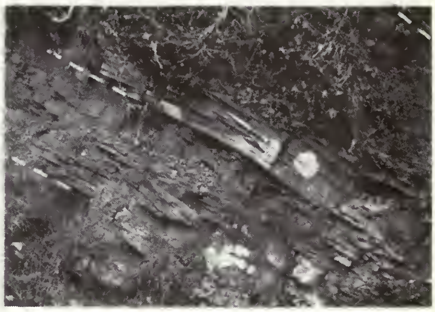

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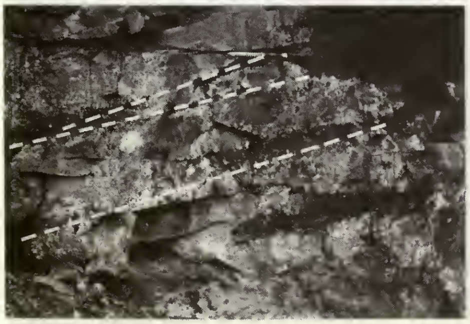

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22

Chatwall Sandstone Formation and Chatwall Limestone Formation with the sequence in the southern area, and the Henley Member of the Acton Scott Formation and its equivalent in the Onny Valley.

a. Base of the Alternata Limestone Formation

In the southern area Bancroft (1929*a*) indicated a stratigraphical break at the base of the Alternata Limestone Formation when he showed that at Soudley it rested on an Upper Soudleyan horizon in the Horderley Sandstone Formation (Fig. 15). Diggens (in discussion to Bassett *et al.* 1966) suggested that a break may occur throughout the Soudley/Cheney Longville area, at the base of the Alternata Limestone Formation, since he had found there phosphatic nodules, set in a yellow sandy limestone, in the basal 1 m. Re-examination of all the available sections confirms this observation. A further problem concerns the upper Horderley Sandstone Formation. In the area of the Onny Valley, the top 15 m contains the *Bancroftina typa* Zone of Bancroft (1933), but at Marshbrook the Alternata Limestone Formation rests directly on Horderley Sandstone Formation containing the *Dalmanella lepta* and *D. indica* Zones of Bancroft (1933). At Soudley the whole of this sequence is missing (Fig. 15). Throughout the whole area the basal part of the Alternata Limestone Formation is condensed or a non-sequence. However, at Soudley phosphatic nodules occur throughout the Alternata Limestone Formation, indicating that there the whole sequence may be condensed.

Hurst (1979) attempts to put the facies and faunal distributions at this horizon into an environmental model. It is apparent that, with these stratigraphic breaks in the Horderley Sandstone Formation, the base of the Alternata Limestone Formation in the Marshbrook and Soudley area could be older than in the Onny Valley. The base at Marshbrook and Soudley may be correlative with the uppermost beds of the Horderley Sandstone Formation (*B. typa* Zone) of the Onny Valley. However, this is thought unlikely for several reasons. The introduction of a distinct fauna dominated by *Heterorthis alternata* and *Trematis punctata* is sudden and in such a localized area as Soudley and the Onny Valley seems more likely to be geologically synchronous. Perhaps the most important consideration is the incorporation of phosphatic nodules in the basal beds of the Alternata Limestone Formation which is probably related to a transgressive event (cf. Cooper 1977), resulting in lack of sediment input into the basin and consequent formation of a condensed sequence.

b. Top of the Alternata Limestone Formation

The thickness of this formation varies, so it is possible that the top is diachronous. At Soudley the formation is only 1·5 m thick and contains phosphatic nodules throughout, possibly because it is condensed and not a result of facies migration as suggested by Hurst (1979). The deposits of the Alternata Limestone Formation are unlike any others in the Caradoc, and possibly indicate an environment influenced by marine bars (Hurst 1979). Thus in such a small geographic area as

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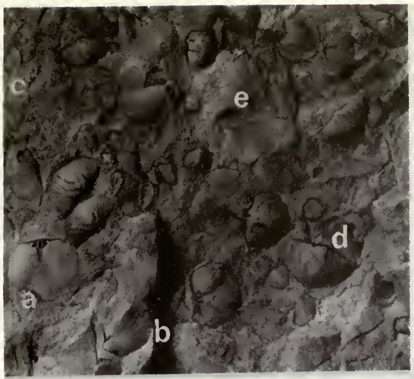
Fig. 23 Shell surface layer (swell lag) from the upper faunal assemblage of the Henley Member of the Acton Scott Formation at SO 449896. a = *Onniella reuschi* b.v., b = *O. reuschi* p.v., c = *Rhactorthis actoniae* b.v., d = *Sowerbyella sericea* p.v. and e = *S. sericea* b.v. ×0·6, BB 73670.

Fig. 24 Shell lag layer from the Alternata Limestone Formation of Soudley Quarry at SO 477918. a = *Heterorthis alternata* p.v., b = *Kjaerina bipartita* p.v., c = *K. bipartita* b.v., d = *Sowerbyella sericea* p.v. and e = *S. sericea.* ×1·2, BB 73668.

Fig. 25 Swell lag from the upper part of the middle faunal assemblage of the Crosspipes Member of the Cheney Longville Formation at Marshwood Quarry, SO 445890 (upper Marshbrookian faunal assemblage). a = *Dalmanella wattsi* p.v., b = *D. wattsi* b.v., c = *Strophomena grandis* p.v., d = prasoporid bryozoan, e = *Tentaculites anglicus,* f = *Brongniartella bisulcata* and g = *Flexicalymene caractaci.* ×1·5, BB 73671.

Fig. 26 Swell lag shell layer from the Ragdon Member of the Acton Scott Formation at SO 451908. a = *Onniella reuschi* p.v., b = ? *Zygospira* sp. b.v., c = *Rhactorthis* cf. *crassa* b.v., d = *Nuculites planulatus,* e = *Similodonta* sp. ×1, BB 73669.

All p.v. = internal moulds of pedicle valves; all b.v. = internal moulds of brachial valves.



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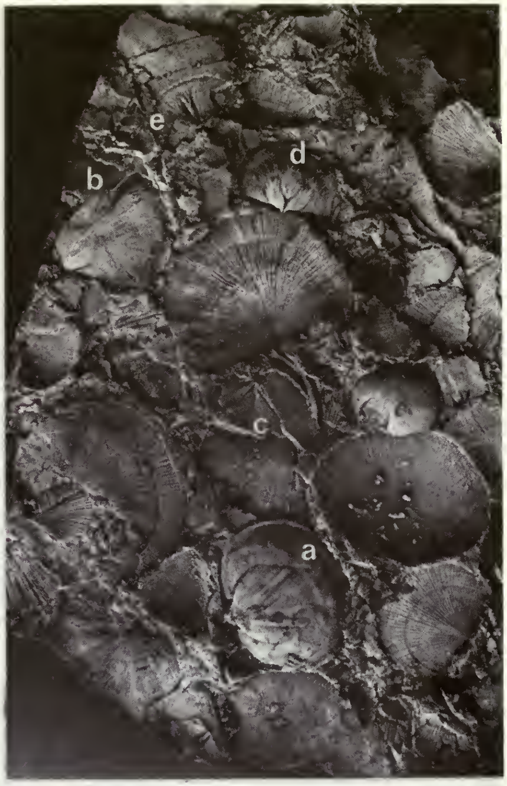

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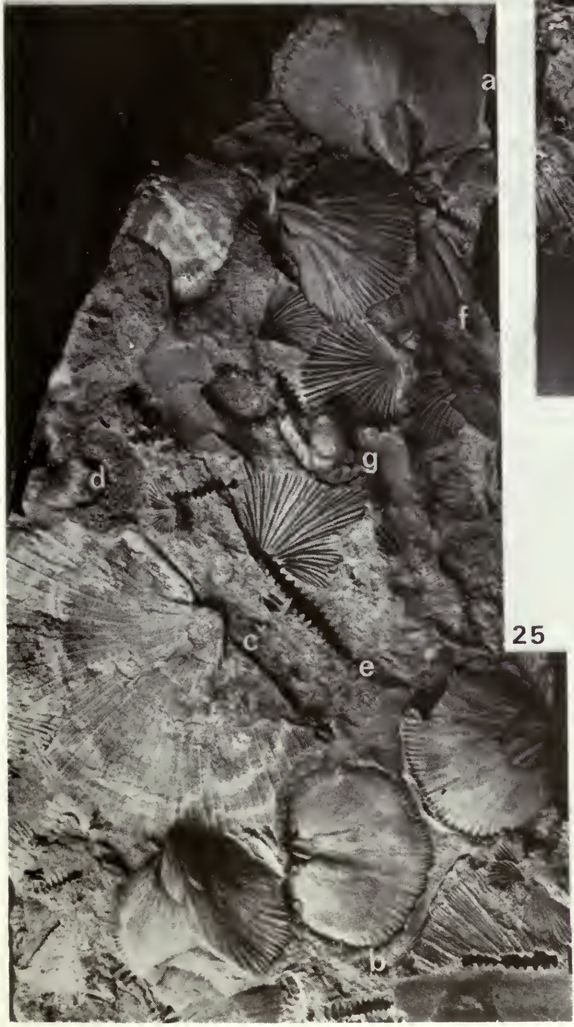

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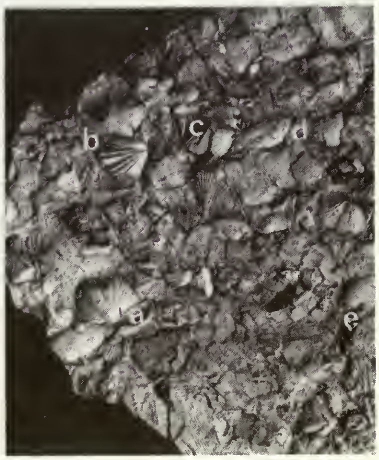

Soudley/Onny Valley, the passing of a peculiar sedimentary environment is likely to be geologically synchronous. However, the attenuated sequence at Soudley could be partly owing to a local facies disturbance such as the migration of marine bars (see Hurst 1979).

Thus it is not known whether the top of the Alternata Limestone Formation and the base of the overlying Cheney Longville Formation is synchronous or diachronous. At Soudley the top might be slightly older, but it is probably synchronous in the rest of the district.

c. Correlation with the Chatwall district

The correlation of the Chatwall Sandstone Formation and Chatwall Limestone Formation with the southern area is difficult. Dean (1960*a*) recognized two stratigraphical breaks in this district, bounding the Chatwall Sandstone Formation (his definition). However, Hurst (1979) has re-analysed these sequences and suggests that the breaks may not exist (see Fig. 15). The evidence for the breaks (Dean 1960*a*) was conglomerate horizons and missing faunal assemblages compared to the Onny Valley sequence. Viewed in the context of sedimentary sequences and environments there is nothing unusual about the conglomerate horizons. They are simply part of a laminated beach environment in which many pebble bed horizons occur (Hurst 1979). Consequently it is not surprising that faunal assemblages are also missing, as the marginal marine environments at Chatwall are different from the open marine equivalents in the Onny Valley.

Based on the evidence of transgressive events (derived from sedimentary criteria) in the Chatwall area, Hurst (1979) suggested that the base of the Chatwall Limestone Formation may correlate in part with the uppermost 15 m of the Horderley Sandstone Formation (*Bancroftina typa* Zone of Bancroft 1933; see Fig. 16). These sediments both indicate a slightly more offshore environment when compared to the immediately preceding strata. This transgressive pulse is the first to reverse the overall regressive nature of the sedimentation patterns in the Soudleyan–Lower

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Fig. 27 *Brongniartella bisulcata.* Internal mould of cranidium, from the Cheney Longville Formation, Crosspipes Member, lowest faunal assemblage, near Cheney Longville. (In.52332, ×1·5.)

Fig. 28 *Chasmops extensus.* Internal moulds of cranidia, from the Crosspipes Member (lower faunal assemblage) of the Cheney Longville Formation at Marsh Quarry, SO 445890. (In.50544, ×1·3.)

Fig. 29 *Kloucekia* (*Phacopidina*) *apiculata.* Internal mould of cranidium, from the Alternata Limestone Formation in Cheney Longville Lane. (In.52157, ×2·3.)

Fig. 30 *Broeggerolithus transiens.* Internal mould of cranidium, from same horizon and locality as Fig. 28. (In.50601, × 2.)

Fig. 31 *Flexicalymene caractaci.* Internal mould of cranidium, from same locality as Fig. 28 but upper faunal assemblage of the Marshbrookian. (In.52230, ×1·5.)

Fig. 32 *Remopleurella burmeisteri.* Internal mould of cranidium, from the Onny Shale Formation at SO 4258 8536. (In.51184, ×3).

Fig. 33 *Primaspis caractaci.* Cranidial plaster cast, from Ragdon Member of Acton Scott Formation at SO 4645 9013. (In.54907, ×2.)

Fig. 34 *Lonchodomas pennatus.* Internal mould of cranidium, from same locality as Fig. 32. (In.37622, ×2·1.)

Fig. 35 *Calyptaulax actonensis.* Cranidial plaster cast, from the Wistanstow Member of the Acton Scott Formation in the Onny Valley. (In.49773, ×2·5.)

Fig. 36 *Onnia superba.* Internal mould of cranidium, from same locality as Fig. 32. (In.14674, ×2.)

Fig. 37 *Onnia cobboldi.* Partially exfoliated cranidium, from Onny Shale Formation at SO 4257 8537. (In.50697, ×2.)

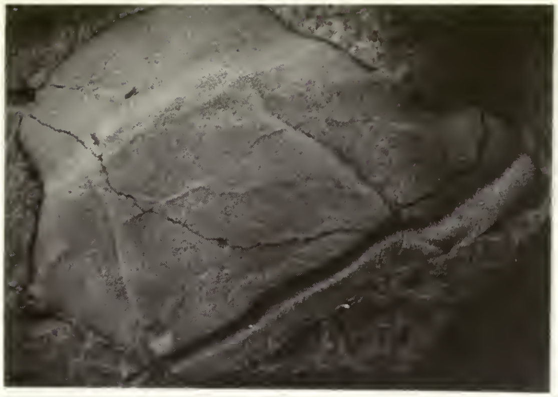
Fig. 38 *Ampyxella edgelli.* Internal mould of cranidium; locality possibly the same as for Fig. 32. (In.48562, ×2.)

Fig. 39 *Chasmops extensus.* Close-up of Fig. 28, ×1·6.

Fig. 40 *Flexicalymene* (*Onnicalymene*) *laticeps.* Cranidium from the Wistanstow Member of the Acton Scott Formation in the Onny Valley. (In.50721, ×2·4).

Fig. 41 *Platylichas laxatus.* Internal mould of cranidium. Acton Scott Formation, Rose Villa, Marshbrook. (In.46446, ×1·6.)

None of the figured trilobites are from the author's collections; some specimens are therefore not located precisely by grid references, as this information was not always available.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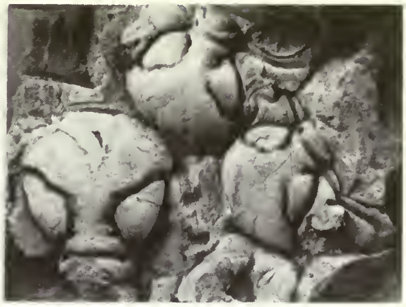
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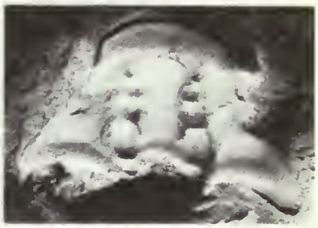
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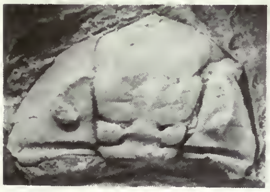
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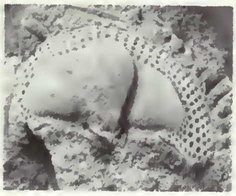
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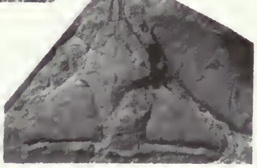
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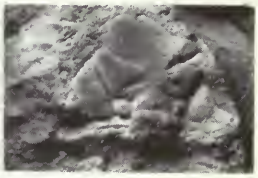
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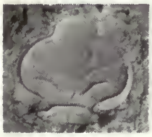
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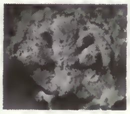
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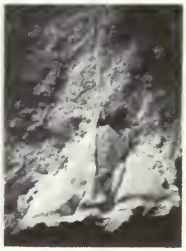
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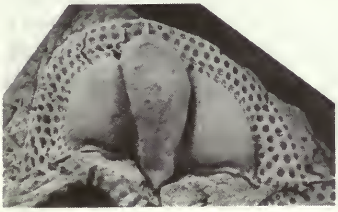
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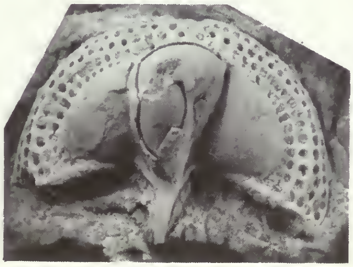
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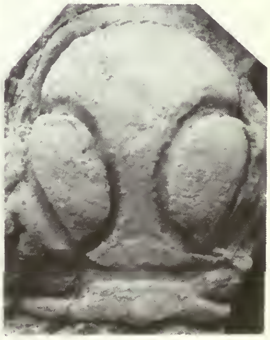
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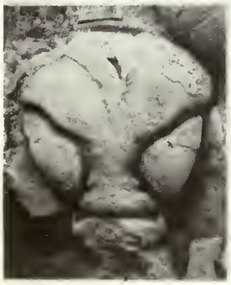
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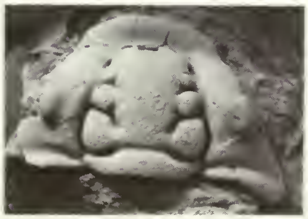
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Longvillian throughout the whole Caradoc area. The non-sequence at Marshbrook and the uppermost part of the one at Soudley, below the Alternata Limestone Formation, could be explained by this transgression (Fig. 15). The condensed sequence at the base of the Alternata Limestone Formation in the Soudley–Onny Valley region may also be a later pulse of the same transgression. If so, the second pulse had a greater effect and marks the beginning of the upper Caradoc transgression which continued to the deposition of the Onny Shale Formation.

Contrary to this, Dean (1958 : 216) argued that the fauna of *Heterorthis alternata*, *Sowerbyella sericea* and *Brongniartella bisulcata* makes it difficult to accept that the Chatwall Limestone Formation is of pre-Upper Longvillian (= Woolstonian) age. Such is not the case if it is accepted that many (if not all) species are facies-correlated, if not facies-controlled. An example of this is seen in the Actonian faunas in which the lowermost faunal assemblage of the Actonian reappears almost species for species with the same sedimentary facies in the upper Actonian Henley Member.

Nearshore sedimentary facies are ephemeral and it is likely that, whatever the relationship of the Alternata Limestone Formation to the Chatwall Limestone Formation, there is little time-difference to effect evolutionary faunal differences. It could be argued that this fauna represents a unique invasion and is likely to be geologically synchronous, but if two distinct transgressive pulses occurred in a short time (Hurst 1979) then two phases of the same faunal invasion could have taken place. Dean (1958, 1960*a*) also argued that the uppermost Chatwall Sandstone Formation had a great deal in common, sedimentologically, with the Chatwall Limestone Formation. Certainly the top 2–3 m of the Chatwall Sandstone Formation forms a sedimentological link with the overlying Chatwall Limestone Formation, but this is no reason to consider it of Woolstonian age or the base of the Chatwall Limestone Formation to be post-basal Woolstonian.

Thus it is considered unlikely that non-sequences occur in the exposed sections of the Chatwall Sandstone Formation. The sediments of the Upper Soudleyan and Lower Longvillian are indicative of a marginal marine environment, compared to the time-equivalents in the Onny Valley, and the attenuated nature of the Chatwall sequence may be simply a result of the differences in sedimentary regime, rather than non-sequences. The age of the base of the Chatwall Limestone Formation is equivocal. Dean (1958) considered that it may be slightly post-basal Upper Longvillian (= Woolstonian). However, his faunal and sedimentological evidence seems inadequate. Following the model proposed by Hurst (1979), it is suggested that the transgressive nature of the base of the Chatwall Limestone Formation correlates with a similar event in the top 15 m of the Horderley Sandstone Formation of the Onny Valley. If so, the top of the Chatwall Limestone Formation (which is not exposed) may be older than the top of the Alternata Limestone Formation and thus the base of the Cheney Longville Formation would be diachronous southwards (see Hurst 1979). This may explain why the Cheney Longville Formation is thickest in the Chatwall region (Greig *et al.* 1968), owing to its earlier initiation.

d. Acton Scott Formation

Following the deposition of the Alternata and Chatwall Limestone Formations, there is a transgression into the farthest-offshore Onny Shale Formation, and it seems probable that the bases of the members and formations are synchronous in such a small area. However, there is difficulty correlating the locally regressive Henley Member with the Onny Valley sequence in the Acton Scott Formation. Dean (1958 : 211) suggested that the stratigraphical position of the Henley Member, with a fauna of *Nicolella actoniae*, *Reuschella bilobata*, *Cryptothyris paracyclica*, *Leptaena*, *Platylichas*, *Chasmops*, *Primaspis* and *Gravicalymene*, supports a correlation with the lower part of the middle Actonian (= lower part of Wistanstow Member) of the Onny Valley. The fauna at the type section for the Henley Member is very similar to the lowest faunal assemblage of the Actonian, but this does not indicate that the Henley Member is lowermost Actonian, as it demonstrably occurs above that fauna in the Acton Scott area. It is arguable whether assemblage stratigraphy of this nature should be used even for local correlations.

Perhaps a more reliable way to attempt to correlate the Henley Member with the Onny sequence can be found by consideration of the sedimentary environments. The Henley Member is a highly calcareous fine sandstone, whilst the Wistanstow Member is a calcareous siltstone. It is possible that the calcareous influx was synchronous. The base of the Henley Member is not exposed so that it is not possible to tie it precisely into the Onny Valley sequence, although it is unlikely to predate the Wistanstow Member, as at least 30 m of the Ragdon Member siltstone is known in the Acton Scott area.

The massive sandstones of the Henley Member are indicative of an environment shallower than the preceding Ragdon Member or the contemporaneous Wistanstow Member, and they suggest a swell or some submarine topographic feature in the Acton Scott area. The formation of such a sediment barrier in an open marine environment is associated with calcareous sediments and may be responsible for the calcareous siltstones of the Onny Valley (cf. Watkins 1979). Thus the removal of the feature would also affect carbonate sedimentation in the district. If such a model is correct then the Henley Member would equate with the whole of the Wistanstow Member of the Onny Valley. The basal Onny Shale Formation has only a small proportion of calcareous material in comparison with the underlying Wistanstow Member, indicating a change in sedimentary conditions such as the destruction of the conditions favourable to the formation of the Henley Member.

Correlation outside the Caradoc district

Within the type area there are many problems with correlation based on shelly faunas. Such faunas are facies-related, creating problems of accurate correlation between the remaining upper Caradoc sequences of the Anglo–Welsh area. Graptolites are of very limited use, not only because they are rare, but also because only two zones are now recognized in the upper Caradoc (Williams *et al.* 1972). Thus correlation with the type area must chiefly be by means of shelly faunas, mainly trilobites and brachiopods, but this creates problems. For instance, Cave (1965) recognized an Onnian fauna in an offshore mud environment in the Welsh Basin. The sedimentary environment is not precisely the same as the type Onnian, but it is very similar. But could this correlation have been effected if the environment happened to consist of nearshore sands, with a related fauna? Not all deposits of Onnian age will be found in offshore environments, but what does a nearshore Onnian fauna consist of?

Another difficulty is the Longvillian sediments of the Bala district in north Wales, which are predominantly muddy (Bassett *et al.* 1966), compared to the sandstones and siltstones of Caradoc. It is no wonder they found little in common for useful correlative purposes, but is the effected correlation correct? The species-similarity within facies may be misleading until more is known about phenotypic variation and ecological clinal variation (cf. Hurst 1978) of the groups involved.

Bancroft (1933) recognized upper Caradoc shelly faunas in the Cross Fell Inlier, which he equated with Longvillian through to the Ashgill. He recognized all the stages and attempted to recognize some of the south Salop zones, and this is the only other area in England or Wales where there is a possible occurrence of a complete upper Caradoc succession. However, in the light of the present work there is a need to revise the fauna completely and to study the sediments, not only to test the proposed correlations but also to ascertain if any stratigraphical breaks occur in the sequence.

Possibly the best marker horizon in the Caradoc is the non-sequence at the base of the Woolstonian. This probably resulted from the initiation of a transgression (Hurst 1979) which carried on into the Onnian. It is traceable into the Welsh Basin (Williams 1953; Cave 1965; Bassett *et al.* 1966) but based on conventional faunal correlations here the non- or condensed sequences last into the Marshbrookian, Actonian or even probably the Onnian. This transgression and production of non- or condensed sequences is obviously a regional event and could possibly prove to be the most widely correlatable horizon of the whole upper Caradoc sequence.

Correlation by means of ash falls is accurate but at the same time limited (Brenchley 1969). The only ash falls in the upper Caradoc are in the lowest faunal assemblage of the Marshbrookian, and there are at least three distinct events which can be pieced together from local sections. None of these ashes is reworked, for they occur in bioturbated beds, not associated with transported sediment. There is no obvious correlative of these ash falls in the Welsh Basin, unless it is argued that the Longvillian ashes of the Bala district (Schiener 1970) are in fact Marshbrookian. When it is considered that the Bala area is correlated with the type section on faunas having very little in common it is difficult to be certain, but no ash falls have been located in any Longvillian or Woolstonian strata in the type Caradoc.

Recent conodont work (Bergström 1964) also highlights correlation problems in the Caradoc. For example, Bergström considered the south Wales Crûg Limestone to be of Marshbrookian age. Very little is known of type Marshbrookian conodonts, mainly owing to the clastic nature of the Caradoc facies. Thus conodont correlation with the type area must be indirect. Williams (1953 : 195) considered the Crûg Limestone to contain a Longvillian–Marshbrookian fauna, 'probably equivalent to the Upper Longville Flags of the Welsh Borders', whereas Williams *et al.* (1972) placed it in the Marshbrookian. The faunal list given by Williams (1953) shows little in common with the type Marshbrookian. Indeed the only species for correlation are the long-ranging *Sowerbyella sericea* and *Nicolella actoniae*, and *Kjaerina geniculata* which is restricted to the Woolstonian (= old Upper Longvillian). This emphasizes that with provincial micro- and macrofaunas (see Williams 1969*a*, *b*, 1972) there is considerable difficulty and ambiguity in correlating with the type sections (see also Dean 1960*c*).

The brachiopod faunas

The last systematic attempt to document type Caradoc brachiopods was undertaken by Bancroft (1928*a*, *b*, 1929*a*, 1933, 1945). Unfortunately, owing to many unhappy circumstances throughout his career, culminating in his premature death in the Second World War in 1944, he never achieved a complete revision of the whole brachiopod fauna. Thus in order to provide a sound basis for the ecological study of the upper Caradoc rocks it is of paramount importance that the taxonomy of this major invertebrate group is well documented.

Approximately 250 collections, numbering some 50,000 fossils, were made in 1974–76 and have been deposited in the British Museum (Natural History). Each collection is referred to by a code, e.g. WFT1, and allocated a locality number with a National Grid Reference. Many separate collections may come from a single locality. The registered numbers of the figured specimens lie within the ranges BB 72243 to BB 72543 and BB 73533 to BB 73646. Specimens in Birmingham University Museum are prefixed by the letters ST and those in the Geological Survey Museum by GSM. With the help of Dr L. R. M. Cocks, lectotypes have been chosen for all of Bancroft's species; the ones not referred to in this study can be found in Cocks (1978). The data of bivariate statistics comprise over 100 tables and are too voluminous to publish; they have therefore been deposited in the Palaeontology Library of the British Museum (Natural History). However, they are to be regarded as an integral part of this study.

Systematic methods

The statistical methods adopted in this paper are those used by Williams (1962, 1963, 1974). Briefly, morphological variation displayed by conspecific specimens is quantified and then samples are tested against one another by standard statistical tests for significance.

Continuous variables are derived by measuring various standard components of the shell (Fig. 42). These are length of valve (l), width of valve (w), depth of valve (d), length of dorsal and ventral muscle scars (lsc), width of muscle scar (wsc), length of dental plates (dl), width of brachiophore bases (wc) and length of septum (ls). Fig. 42 indicates where typical measurements were taken.

Such parameters are bivarately analysed by the reduced major axis method, to find correlations and express growth ratios. Differences in such parameters as growth ratios (a or α) are tested for significance. Continuous univariate characters, such as the wavelength of ribs at a given distance anteromedially of the umbo, are assumed to be normally distributed and compared by the t test. Discontinuous univariate characters, such as the relative branching of costellae enumerated

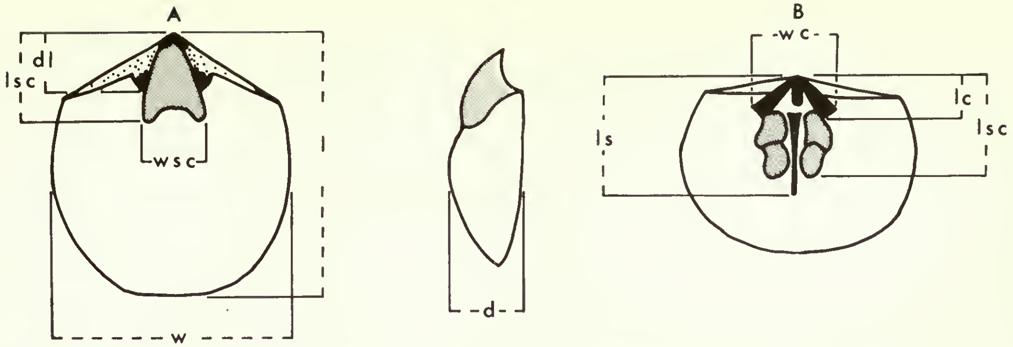


Fig. 42 Schematic representation of moulds of pedicle (A) and brachial (B) valves, showing measurements taken.

according to Bancroft's notation (Bancroft 1928*a*), have been compared by χ^2 tests, contingency, or 2 × 2 tables, depending on the sample size.

Generally if there are significant differences (at least at the 95% level) in two or more characters between two separate samples they are treated as belonging to two separate taxa.

All measurements given for length and width of figured material are in mm.

Localities

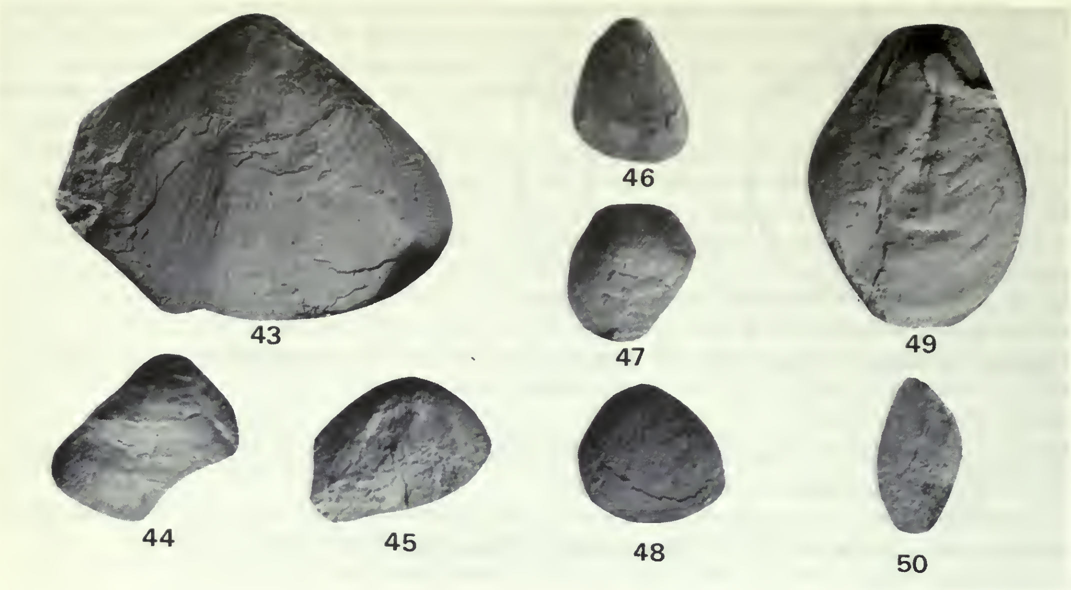
Listed below are the localities from which the specimens, forming the basis of this work, were collected. Following each locality number is the stratigraphic horizon, the National Grid Reference and a short geographical description. Bancroft's localities (1949) are listed where appropriate. Many separate collections derive from a single locality and where appropriate these are mentioned throughout the text.

Alternata Limestone Formation

1. SO 4158 8524. Roadside exposures (north side) 500 m NW of the motte and baily at Cheney Longville.
2. SO 4180 8571. Under both banks of the River Onny, immediately W of footbridge.
3. SO 4182 8569. On the north bank of the River Onny, immediately E of footbridge.
4. SO 4180 8565. Intermittent exposure for 50 m in the south bank of the old Bishops Castle railway cutting.
5. SO 4227 8733. In the roadside immediately SE of Woolston Quarry.
6. SO 4403 9050. Exposure for 45 m in west bank of railway cutting, 650 m N of Marshbrook Station.
7. SO 4772 9182. Soudley Quarry.
8. SO 5137 9741. At the road junction and in the road leading into Chatwall Hall.

Cheney Longville Formation: Glynboro Member

9. SO 4770 9120. Exposure in stream bed SW of Soudley Quarry.
10. SO 4177 8507. Continuous roadside exposure, 250 m NW of the motte and bailey at Cheney Longville.
11. SO 4190 8493. On the eastern side of the road, immediately W of the motte and bailey at Cheney Longville.
12. SO 4207 8546. Large old river cliff; the same beds are exposed in a farm track immediately to the SW.
13. SO 4190 8572. Small roadside quarries, obscured by undergrowth, approximately 250 m SE of New House.
14. SO 4230 8730. On the south side of the road, intermittent exposures 130 m NE of the road junction at Woolston.
15. SO 4357 8922. In the lane 500 m NE of Whittingslow; intermittent exposure for 45 m.
16. SO 4772 9182. Soudley Quarry.



Figs 43–50 *Obolus* sp., exfoliated brachial valves: 43 = BB 72247, ×2·2; 44 = BB 72248, ×3·2; 45 = BB 72246, ×2·3. *Obolus salopiensis* sp. nov., **holotype,** exfoliated pedicle valve: 46 = BB 72243, ×4; exfoliated brachial valves: 47 = BB 72244, ×4·3; 48 = BB 72245, ×6·6. *Lingulella* sp., exfoliated brachial valves: 49 = B 24201, ×3·8; 50 = BB 72249, ×4.

17. SO 4778 9159. In the stream S of Soudley Quarry.
18. SO 4790 9159. Small roadside exposure SE of Soudley Quarry.

Cheney Longville Formation: Crosspipes Member

19. SO 4190 8493. On the eastern side of the road, immediately W of the motte and bailey at Cheney Longville.
20. SO 4215 8548. In the bed of the River Onny; underwater exposure.
21. SO 4224 8542. River cliff on south side of River Onny; exposure for 50 m, due E of Burrells Coppice.
22. SO 4225 8542. Temporary exposure at end of river cliff on south side of River Onny. Loc. P8 of Bancroft.
23. SO 4240 8725. On the south side of the road, intermittent exposures 50 m NE of the road junction at Woolston.
24. SO 4245 8724. Temporary exposure behind house, immediately N of road junction at Woolston.
25. SO 4250 8729. Outcrop at the junction of the lanes from Woolston to Whittingslow and from Woolston to the Corner, 100 m NE of the T-junction at Woolston.
26. SO 4224 8914. Stream section 750 m due S of Marshbrook.
27. SO 4446 8901. Quarry in Marsh Wood, 740 m due S of Marshbrook.
28. SO 4448 8900. Trackside exposure from Marsh Wood Quarry.
29. SO 4472 8887. Bank of Quinny Brook 350 m SE of Marsh Wood Quarry.
30. SO 4406 8976. Quarry on the south side of the road 180 m WSW of Marshbrook Station.
31. SO 4377 8966. Exposure on the south side of the road 550 m WSW of Marshbrook Station.
32. SO 4398 9002. Roadside exposure 350 m NE of Marshbrook Station on the Marshbrook–Minton road.
33. SO 4507 9094. Stream exposures 300 m S of The Hough.

Acton Scott Formation

34. SO 4230 4040. Under tree roots in abandoned meander of River Onny. Loc. P7 of Bancroft.
35. SO 4252 8600. Small disused quarry next to small stream in Dandy Hollow.
36. SO 4238 8538. Small exposure on south bank of River Onny, partly submerged and at exit of abandoned meander. Locs Pa2 and Pa6 (= Pa′ ′ ′) of Bancroft.

37. SO 4238 8538. Crumbling riverbank exposure on south side of River Onny and submerged outcrops in river bed.
38. SO 4240 8538. Partly submerged mudstone ledge on south bank of River Onny. Loc. Pa of Bancroft.
39. SO 4241 8538. Partly submerged mudstone ledge, next to dead tree lying across river, on south side of River Onny. Loc. Pm3 of Bancroft.
40. SO 4248 8538. Submerged mudstone ledge on north side of River Onny. Loc. Py2a of Bancroft.
41. SO 4249 8538. Submerged mudstone ledge on north bank of River Onny. Locs Py2g and Py3 of Bancroft.
42. SO 4450 8964. In south bank of boggy stream in wood due E of Rose Villa.
43. SO 4460 8992. Exposure in overflow channel at Chuney Pool, 400 m S of Oakwood.
44. SO 4505 9053. Intermittent exposures in stream between 400 m and 700 m S of The Hough.
45. SO 4645 9013. Exposure in south bank of stream, 1300 m ENE of Acton Scott.
46. SO 4645 9025. Intermittent exposures in tributary streams 120 m N of roadbridge.
47. SO 4496 8955. Disused overgrown quarry 500 m W of Acton Scott Church.
48. SO 4548 8928. Exposure in rock garden of Acton Scott Hall.

Onny Shale Formation

49. SO 4254 8538. Continuous exposure in riverbed of Onny River. Locs Pw1, Pw3 and Pw5 of Bancroft.
50. SO 4257 8537. Continuous exposure in riverbed of Onny River. Loc. Pc of Bancroft denotes base of outcrop.
51. SO 4258 8536. River cliff on north bank of River Onny. Including locs P2 and P3–5 of Bancroft.

Systematic palaeontology

Class **INARTICULATA** Huxley, 1869
Order **LINGULIDA** Waagen, 1885
Superfamily **LINGULACEA** Menke, 1828
Family **OBOLIDAE** King, 1846
Subfamily **OBOLINAE** King, 1846

Genus ***OBOLUS*** Eichwald, 1829

Obolus salopiensis sp. nov.
Figs 46–48

Description. Dorsibiconvex, subcircular to subtriangular *Obolus* with a mean length relative to width of 93% (range 90% to 94%) and a mean depth relative to length of 11% (range 9% to 12%) for 4 pedicle valves, and a brachial valve 94% as long as wide and 18% as deep as long; both valves strongly convex laterally but flattened medially and anteriorly; shell surface ornamented by very fine concentric growth lines and impersistent low rounded plicae especially on anterior flanks.

Pedicle valve with striated, lenticular pseudointerarea, orthocline in attitude, divided into two propareas by a shallow pedicle groove which is 7·5% (range 6·5% to 8% for 4 valves) as wide as valve length; ventral muscle impressions unknown.

Brachial valve with small striated triangular pseudointerarea, orthocline to anacline in attitude; dorsal muscle impressions unknown.

Name. From the County of Salop (Shropshire).

Material. Holotype, partially exfoliated pedicle valve (BB 72243), length 2·8 mm, width 2·9 mm. Paratypes, partially exfoliated brachial valves (BB 72244–5), length 3·0 and 3·8 mm, width 3·3 and 4·2 mm. Type material from loc. 45. Also occurs at locs 35, 36, 43, 44 and 49.

Discussion. This small oboloid occurs sporadically in the Acton Scott Formation and in the lower part of the Onny Shales. Only two small samples, one from each stratigraphic level, were available for bivariate study (Tables 1, 2).* Comparison of dorsal outline of the two samples

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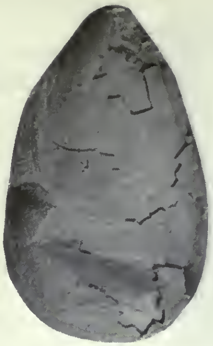
*The tables of bivariate statistics are deposit data available in the Palaeontology Library of the British Museum (Natural History); see p. 220.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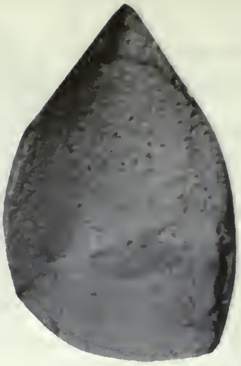
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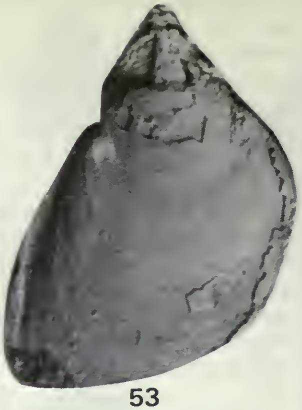
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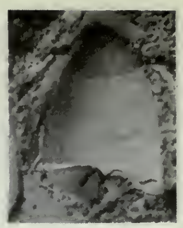
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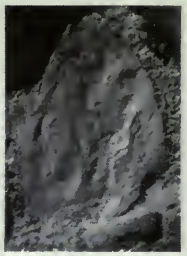
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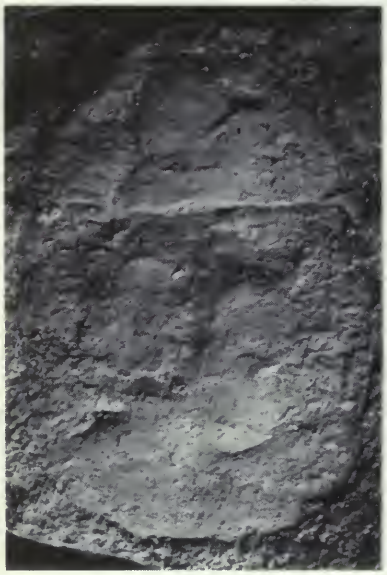
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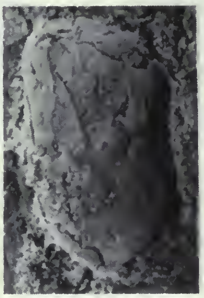
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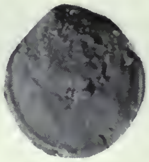
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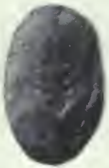
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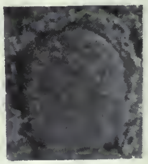
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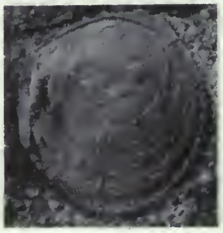
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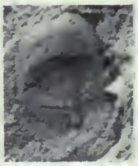
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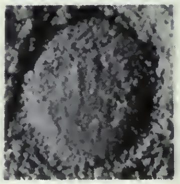
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Figs 51–63 *Palaeoglossa lockleyi* sp. nov., pedicle valves: 51 = BB 72250, ×2·7, 52 = **holotype** BB 72251, ×5·2, 53 = BB 72252, ×5·2; brachial valves: 54 = BB 72253, ×5·4, 55 = BB 72254, ×4. *Pseudolingula* sp., articulated specimen: 56 = BB 72255, ×4·4. *Paterula* cf. *subcircularis*. pedicle valves: 57 = BB 72258, ×12·5, 59 = BB 72257, ×12; brachial valves: 58 = BB 72259, ×10·5, 60 = BB 72260, ×13. *Paterula* sp., brachial valve: 61 = BB 72261, ×7. *Lingulops* sp., brachial valve: 62 = BB 72264, ×7. *Elliptoglossa* sp.: 63 = BB 72263, ×3·3.

shows a significant difference ($P < 0{\cdot}01$), with more rounded individuals occurring in the Onny Shales. However, other morphological attributes show no significant differences. The difference in dorsal outline is not sufficient to recognize taxonomically, and thus the samples are thought to indicate the presence of only one morphological species. *O. salopiensis* is closely related to *O. subditivus* Williams but differs in its more triangular shell configuration, shallower pedicle valve and deeper brachial valve. In assigning *O. subditivus* to the obolids, Williams indicated (1974 : 26) that it was a matter of convenience until more was known about the musculature. Similarly, nothing is known about the musculature of *O. salopiensis* so it too is provisionally assigned to the obolids.

Obolus sp.
Figs 43–45

Several exfoliated brachial valves (BB 72246–8) of a large *Obolus* have been obtained from the arenaceous sediments of the Acton Scott Formation at loc. 47. The valves are evenly convex, subtriangular, with a mean length relative to width of 93% (range 85% to 100% for 3 valves) and a mean depth relative to width of 19% (range 15% to 24% for 2 valves). One valve (BB 72246) shows a pair of oval posterior muscle scars but there is no indication as to whether they are transmedian or lateral scars. Shell surface appears to be ornamented by low concentric undulations. The length ranges from 7·1 to 20·0 mm and the width from 8·5 to 24·0 mm.

Subfamily **LINGULELLINAE** Schuchert, 1893

Genus ***LINGULELLA*** Salter, 1866

Lingulella sp.
Figs 49, 50

A few brachial valves of a small *Lingulella* have been recovered from the uppermost Onny Shales at loc. 50. A single brachial valve (B 24201; length 12·2 mm, width 8·2 mm), from the Onny river cliff (loc. 51) occurs in the G. H. Morton collection of the British Museum (Natural History). The valves are elongately oval and 69% as wide as long (range 68% to 70% for 3 valves). One valve was 11% as deep as long. Shell surface ornamented by very fine concentric growth lines. Visceral area strongly pustulose. Owing to the lack of well-preserved material no information is available on the pseudointerareas or muscle configuration, thus precluding specific identification of the specimens.

Genus ***PALAEOGLOSSA*** Cockerell, 1911

Palaeoglossa lockleyi sp. nov.
Figs 51–55

DESCRIPTION. Dorsibiconvex oval to elongately oval *Palaeoglossa* with a brachial valve 67% as wide as long and 15% as deep as long (range 13% to 18% for 3 valves); pedicle valve 70% as wide as long and 7% as deep as long (range 6% to 7% for 3 valves); both valves evenly convex, ventral beak not incurved, dorsal beak rounded and incurved; shell surface ornamented by very fine concentric growth lines.

Crescentic ventral pseudointerarea striated, anacline in attitude, 16% as long medially (range 12% to 21%) and 20% as long laterally (range 17% to 21%) as the length of the valve, for three specimens; pedicle trough narrow and shallow; nature of ventral muscle field unknown.

Very small, anacline, dorsal pseudointerarea; muscle field configuration unknown.

NAME. After Dr M. G. Lockley.

DIMENSIONS.	length	width
Internal mould of pedicle valve, BB 72251, holotype	8·4	5·9
Partially exfoliated pedicle valve, BB 72250	16·5	10·2
Partially exfoliated pedicle valve, BB 72252	9·0 (est.)	8·0
Partially exfoliated brachial valve, BB 72253	4·5	3·5
Partially exfoliated brachial valve, BB 72254	7·0	5·0

HORIZON AND LOCALITIES. Type material from loc. 44, except paratype BB 72250 from loc. 26. Also recorded from locs 35, 36, 43 and 45.

DISCUSSION. A small sample of *P. lockleyi* has been recovered from the Acton Scott Beds to give some indication of shape variability (Tables 3, 4). Comparison of the brachial valve outline with *P. attenuata* (Sowerby), from the Llandeilo Meadowtown and Rorrington Beds of the Shelve district (see Williams 1974 : 34), indicates no significant difference. Comparison of the pedicle valve shape shows that *P. lockleyi* differs significantly ($P < 0{\cdot}05$) from *P. attenuata* from the

Meadowtown Beds but not from the other samples of *P. attenuata* from the Rorrington Beds and the Upper Llanvirn Betton Beds. *P. lockleyi* and *P. attenuata* further differ in that the former has a deeper brachial and pedicle valve. Also, the pedicle trough of the new species is significantly longer and the ornament consists solely of fine concentric growth lines, there being no indication of fila as in *P. attenuata*.

Subfamily **GLOSSELLINAE** Cooper, 1956

Genus ***PSEUDOLINGULA*** Mickwitz, 1909

Pseudolingula sp.

Fig. 56

Four fragmentary specimens from the Crosspipes Member at Marshwood Quarry (loc. 27) and one from the Acton Scott Formation (loc. 44) are the sole representatives of *Pseudolingula* in the Upper Caradoc. A relatively complete articulated specimen (BB 72255) was 14·5 mm long and 10·mm wide with a biconvex parallel-sided shell. Shell surface appears to have been smooth.

Family **PATERULIDAE** Cooper, 1956

Genus ***PATERULA*** Barrande, 1879

Paterula cf. ***subcircularis*** Cooper

Figs 57–60

1956 *Paterula subcircularis* Cooper : 239–240; pl. 24, figs 7–10.

Description. Shallow biconvex subcircular *Paterula* with a brachial valve 95% as wide as long and a pedicle valve 93% as wide as long; shell surface ornamented by very fine concentric growth lines; width of shallow pedicle notch 5% of the length of the valve and situated immediately posterior to the ventral beak which is submarginal and located at 12% of the length of the valve; submarginal dorsal beak, located at 11% of the length of the brachial valve.

Well-defined limbus 7% (range 4% to 10% for 7 valves) and 8% (range 5% to 10% for 9 valves) as wide as the pedicle and brachial valves are long, respectively. Pedicle valve with extremely faint short median ridge extending anteriorly from pedicle notch; two lines diverge anteriorly from the beak.

Horizon and localities. All specimens from the basal Onny Shale Formation; loc. 49. Representative dimensions of pedicle valves: BB 72257, length 1·3 mm, width 1·3 mm; BB 72258, length 2·1 mm, width 2·0 mm. Brachial valves: BB 72259, length 2·0 mm, width 2·0 mm; BB 72260, length 1·1 mm, width 1·1 mm.

Paterula sp.

Fig. 61

Several internal brachial moulds of a paterulid (e.g. BB 72261, length 1·8 mm, width 1·4 mm) have been recovered from the Acton Scott Formation at loc. 44. Two valves were on average 74% as wide as long with a limbus 10% as wide as the valves are long, and a submarginal dorsal beak located at 14% of the length of the valve. Internal features unknown.

Discussion. The Caradoc *Paterula* belong to two distinct species. The sample from the Onny Shale Formation was used to derive the statistics in Tables 5–7. The species is comparable with *P. subcircularis*, described by Cooper (1956 : 239) from the Springtown Shale of Oklahoma, in the near-circular valve shape and shallow biconvexity. However, the Caradoc specimens differ from the large *P. subcircularis* in their small size and in having a shallow pedicle notch as opposed to a deep one. These minor morphological differences do not justify the erection of a new species. No useful purpose is served in comparing the scarce *Paterula* sp. with described species.

Genus *ELLIPTOGLOSSA* Cooper, 1956

Elliptoglossa sp.

Fig. 63

A single articulated specimen (BB 72263) from the Acton Scott Formation at Chuney Pool (loc. 43) is provisionally assigned to *Elliptoglossa*. The shallow biconvex shell was 4·8 mm long and 4·2 mm wide, with a subelliptical outline and a shell surface ornamented by very fine growth lines.

Genus *LINGULOPS* Hall, 1872

Lingulops sp.

Fig. 62

Complementary moulds of a brachial valve (BB 72264) from a temporary exposure in the Crosspipes Member at loc. 24 are the sole representatives of the genus in the Upper Caradoc. The valve, which had a subelliptical outline, was 3·5 mm long, 2·2 mm wide and 0·5 mm deep, with a submarginal beak located 1 mm from the posterior margin. Muscle field anteriorly impressed. Shell surface ornamented by very fine growth lines.

Family CRANIOPSIDAE Williams, 1963

Genus *PARACRANIOPS* Williams, 1963

Paracraniops doyleae sp. nov.

Figs 64–69

Description. Oval, subequivalve *Paracraniops* with a dorsal (?) valve 81% as wide as long and 17% as deep as long; transverse profile evenly convex, longitudinal profile eccentrically convex with a submarginal apex slightly overhanging a truncated posterior margin with a small groove; anteriorly flattened. Ventral (?) valve 82% as wide as long and 14% as deep as long; transverse and longitudinal profiles, and apex and posterior margin characteristics as for dorsal (?) valve. Valve edges with small flange about 7% length of valve. Shell surface ornamented by lamellose growth lines which become widely spaced anteromedially.

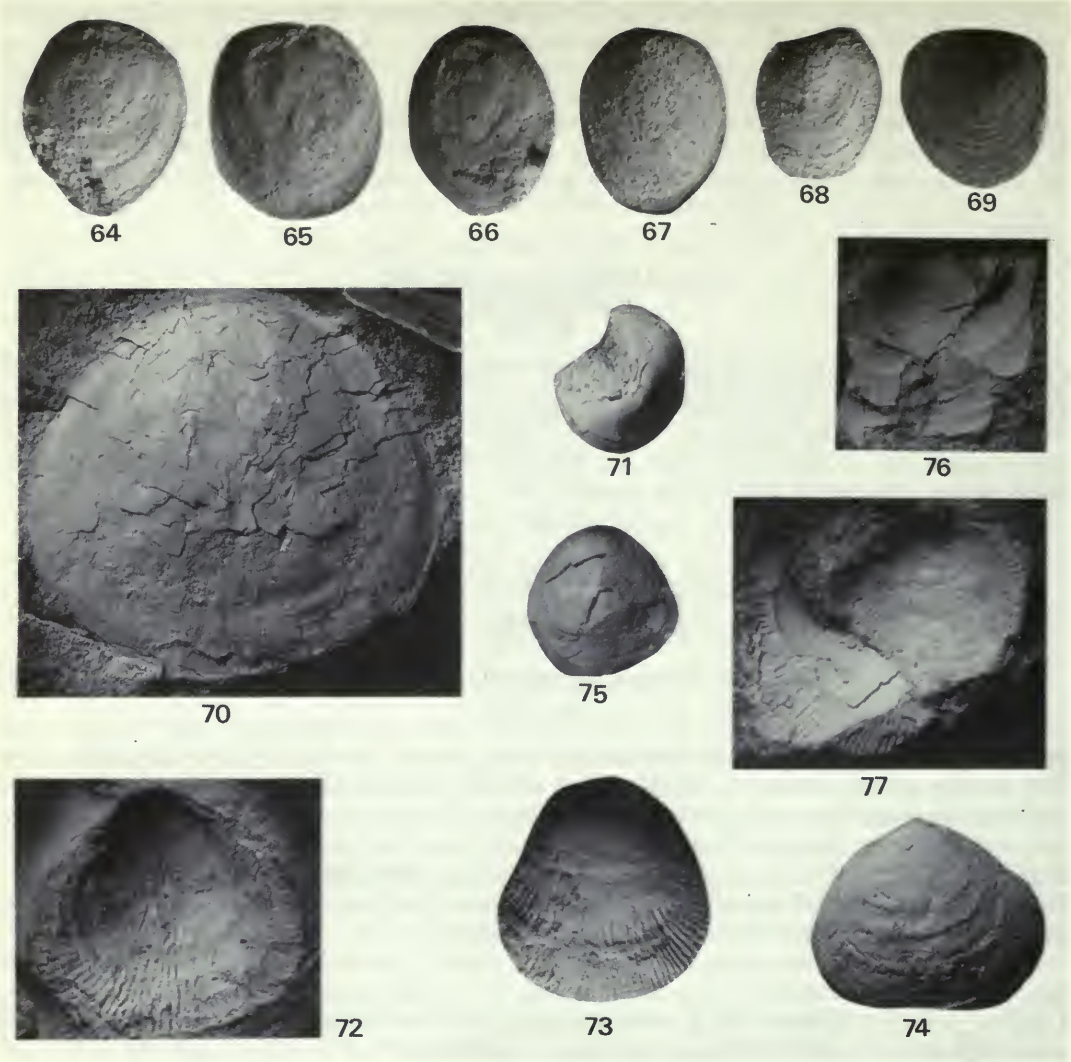
Ventral (?) interior with elongate, semicircular, slightly elevated platform, with well-defined periphery, extending anteriorly from the valve apex for 60% the length of the valve, and containing a pair of posterior adductor scars diverging widely at over 100° from the valve apex, bounded anterolaterally by a pair of elongate oval anterior adductor scars; centre of platform accommodating elongate peardrop-shaped oblique internal scar.

Dorsal (?) interior with two very poorly defined ridges extending from the valve apex for approximately three-quarters of valve length to the edge of the poorly-defined anterior adductor scar. Posterior adductor and oblique internal scars very poorly developed but appearing to diverge widely from valve apex.

Name. After Ms M. C. Doyle.

Dimensions.	length	width
Internal mould of pedicle valve, BB 72278, holotype	4·5	4·0
Internal mould of pedicle valve, BB 72279	4·3	3·5
Internal mould of pedicle valve, BB 72280	4·0	3·3
Internal mould of brachial valve, BB 72281	4·5	4·0
Internal mould of brachial valve, BB 72282	3·5	3·0
External mould of brachial valve, BB 72283	4·5	3·9

Horizon and localities. Type material from loc. 44. Also recorded from locs 11, 12, 15, 19, 24, 26, 30, 32, 34, 35, 43, 45, 46, 47 and 48.



Figs 64–77 *Paracraniops doyleae* sp. nov., internal moulds of pedicle (?) valves: 65 = **holotype** BB 72278, ×6·2, 67 = BB 72279, ×6, 66 = BB 72280, ×6; internal moulds of brachial valves: 64 = BB 72281, ×6, 68 = BB 72282, ×6, 69 = BB 72283, ×5. *Trematis punctata* (J. de C. Sowerby): 70 = brachial valve BB 54739, ×3, 71 = pedicle valve BB 72256, ×1·5. *Schizocrania salopiensis* Williams, brachial valves: 72 = BB 24955, ×3·5, 73 = BB 24953, ×3, 74 = BB 30077, ×3·5, 75 = BB 72265, ×3·5, 76 = BB 72266, ×2·5, 77 = BB 72267, ×3·5.

DISCUSSION. *Paracraniops* occurs sporadically, but occasionally locally very abundantly, throughout the Cheney Longville Formation and the Acton Scott Formation. Only material from the Acton Scott Formation was well enough preserved for statistical analysis, the results of which are presented in Tables 8–12. The *Paracraniops* from the Cheney Longville Formation is considered conspecific with *P. doyleae*. The Salopian *Paracraniops* is closely related to *P. macella* Williams, which is known from the older Longvillian (Gelli-grîn Ashes) rocks of Bala, north Wales (Williams 1963 : 346–349). They principally differ in that the former is more transverse and has a brachial valve deeper than the pedicle valve. Further, in the ventral (?) interior of *P. doyleae* the posterior adductor scars are obtusely splayed and in the dorsal (?) interior the ridges more widely splayed.

Order **ACROTRETIDA** Kuhn, 1949
Suborder **ACROTRETIDINA** Rowell, 1949
Superfamily **DISCINACEA** Gray, 1840
Family **TREMATIDAE** Schuchert, 1893

Genus *TREMATIS* Sharpe, 1848

Trematis punctata (J. de C. Sowerby)

Figs 70, 71

1839 *Orbicula granulata* J. de C. Sowerby *in* Murchison : 636.
1839 *Orbicula punctata* J. de C. Sowerby *in* Murchison : pl. 20, fig. 5.
1866 *Discina* (*Trematis*) *punctata* (J. de C. Sowerby) Davidson : 69; pl. 6, fig. 9.

DESCRIPTION. Subcircular, gently convex brachial valve (e.g. BB 54739, length 18·1 mm, width 19·2 mm), about one-sixth as deep as long with maximum depth posteriorly; small dorsal umbo but no pseudointerarea observed on specimens available. Ornament of small hexagonal pits arranged consistently in a hexagonal megapattern. Dorsal interior posteriorly thickened with shallow broad median ridge separating two very shallow oval muscle scars.

Pedicle valve evenly convex, depressed posteriorly, with eccentric beak and open triangular pedicle notch.

HORIZON AND LOCALITIES. Occurs at locs 1, 2, 3, 4, 5, 6, 7 and 8. Lectotype (selected Cocks 1978, not figured here) GSM 6878, from Cheney Longville Formation west of Church Preen.

DISCUSSION. Wright (1963) analysed the pit arrangement of *Trematis*. *T. punctata* has hexagonally arranged pits, and is similar to *T. millepunctata* Hall and *T. craigensis* Reed.

Genus *SCHIZOCRANIA* Hall & Whitfield, 1875

Schizocrania hewardi sp. nov.

Figs 78–83

DESCRIPTION. *Schizocrania* with subcircular brachial valve, 97% as long as wide and 23% as deep as long, transverse and asymmetric profiles evenly convex; umbo posteriorly placed overhanging straight truncated posterior margin with a strong groove; shell surface ornamented by faint persistent growth lines and straight radial capillae.

Dorsal interior with small elongately oval, widely divergent, posterior adductor scars, weakly impressed and extending anteriorly from the posterior margin for 23% of the length of the valve; anterior adductor not impressed; pedicle valve unknown.

NAME. After Dr A. P. Heward.

DIMENSIONS.	length	width
Exterior of brachial valve, BB 72268, holotype	1·2	1·3
Exterior of brachial valve, BB 72269	1·0	1·2
Exterior of brachial valve, BB 72270	1·1	1·2
Exterior of brachial valve, BB 72271	1·1	1·2

HORIZON AND LOCALITY. All the material from the upper part of the Onny Shale Formation, from the Onny river cliff; loc. 51.

Schizocrania salopiensis Williams

Figs 72–77

1974 *Schizocrania salopiensis* Williams : 44–46; pl. 6, figs 22–26.

DESCRIPTION. *Schizocrania* with subcircular to subelliptical or subtriangular brachial valve, 95% as long as wide and 29% as deep as long, evenly convex in both transverse and longitudinal profile; submarginal umbo not overhanging smoothly rounded posterior part of valve; shell surface ornamented by very faint impersistent growth lines and radial capillae, which branch dichotomously and curve towards the anterior and lateral margins.

Dorsal interior with large slightly divergent subcircular to oval posterior adductor scars, weakly impressed and extending anteriorly from the posterior margin for 29% of the length of the valve; small circular anterior adductor scars situated near the centre of the valve and separated by a very shallow median ridge; pedicle valve unknown.

Horizon and localities. BB 72265–7 are from loc. 44; BB 24953, BB 24955 and BB 30077 from loc. 27. Also recorded at locs 36 and 45. Dimensions of brachial valves ranged from BB 72265, with length 4·6 mm and width 5·5 mm, to BB 24953, length 12·6 mm and width 10·4 mm.

Discussion. *Schizocrania* brachial valves are fairly common in the Upper Caradoc rocks, which have provided two samples used to derive the statistics given in Tables 13–15. Data on shell shape, depth and length of posterior adductor scars show that *S. hewardi* differs from *S. salopiensis* Williams (1974 : 46) in valve shape ($P < 0{\cdot}01$) and length of the posterior adductor scars ($P < 0{\cdot}05$). They do not differ in shell depth. Further, *S. hewardi* has an incurved posteriorly-placed umbo along a straight truncated valve margin with a strong groove, whilst *S. salopiensis* has a rounded posterior profile without an overhanging umbo. The posterior adductor scars of *S. hewardi* are also more widely splayed.

S. hewardi differs from *S. salopiensis* Williams, from the Upper Llandeilo Rorrington Beds of the Shelve district, in terms of valve shape ($P < 0{\cdot}001$), depth ($P < 0{\cdot}001$) and length of posterior adductor scars ($P < 0{\cdot}05$). From the younger sample of *S. salopiensis* from the Lower Caradoc Spy Wood Grit *S. hewardi* differs in valve shape ($P < 0{\cdot}001$) and length of posterior adductor scars ($P < 0{\cdot}05$). There is no difference in valve depth of the two species. Such differences are considered sufficiently important to warrant the erection of a new species, even though no pedicle valves of either species have yet been recovered.

The *Schizocrania* from the Crosspipes Member and Acton Scott Formation is similar to *S. salopiensis* in respect of its rounded rather than truncated posterior margin and submarginal umbo. However, it differs significantly ($P < 0{\cdot}05$) from both the Spy Wood Grit and Rorrington Beds samples of *S. salopiensis* (see Williams 1974 : 46) in shell shape as it grew longer relative to width. This difference is not considered sufficiently important to warrant the erection of a new species.

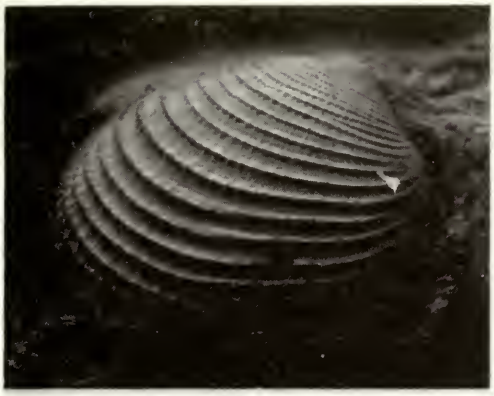
Family **DISCINIDAE** Gray, 1840
Subfamily **ORBICULOIDEINAE** Schuchert & Le Vene, 1929

Genus ***ORBICULOIDEA*** d'Orbigny, 1847

Orbiculoidea ovata sp. nov.
Figs 84–88

Description. Biconical, subcircular to suboval *Orbiculoidea* with a brachial valve on average 92% as wide as long (range 76% to 99% for 5 valves), 27% as deep as long (range 27% to 31% for 5 valves); transverse profile evenly convex, longitudinal profile eccentrically convex with a beak located on average 37% (range 29% to 41% for 5 valves) of the length of the brachial valve; pedicle valve on average 86% as wide as long (values for 2 valves 80% and 92%), 23·5% as deep as long (values for 2 valves 23% and 24%); transverse profile evenly convex, longitudinal profile eccentrically convex with a conical beak located 39% (value for 2 valves 39% each) of the length of the pedicle valve, which is flattened anteriorly; surface of both valves ornamented solely by coarse well-rounded concentric growth lines.

Figs 78–83 *Schizocrania hewardi* sp. nov., all brachial valves: 79 and 81 = **holotype**, BB 72268, viewed from above and obliquely, ×75; 78 and 80 = BB 72271, viewed half obliquely and from side, ×75 and ×100 respectively; 82 = BB 72269, partly exfoliated valve viewed from above, ×100; 83 = oblique enlargement of ornament on BB 72271, ×400. Figs 78–83 are all stereoscan photomicrographs with approximate magnifications.



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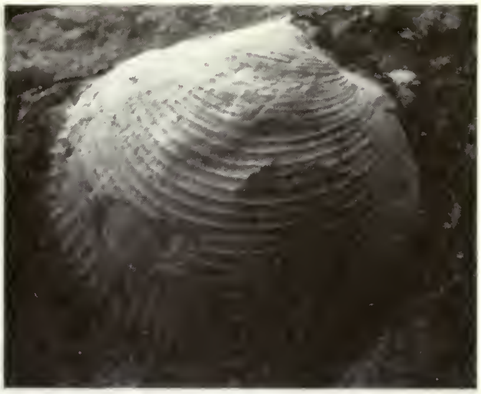

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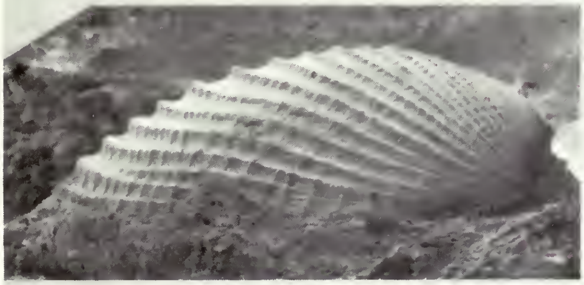

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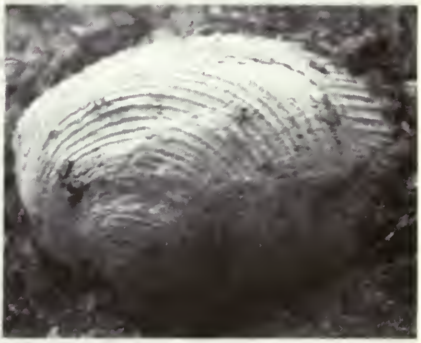

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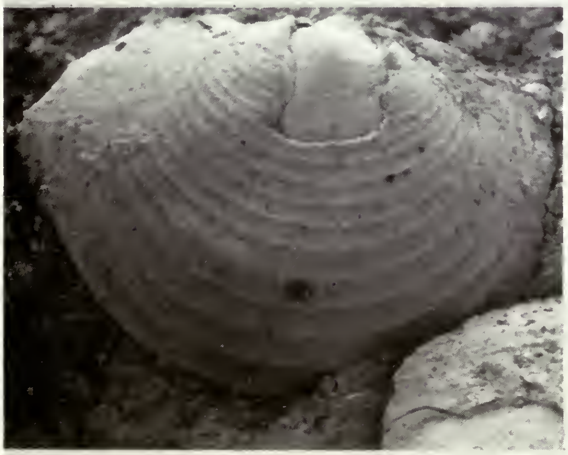

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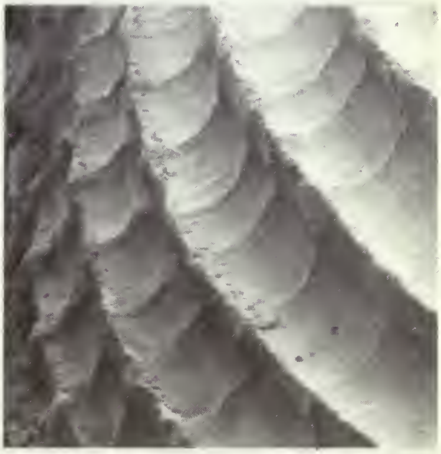

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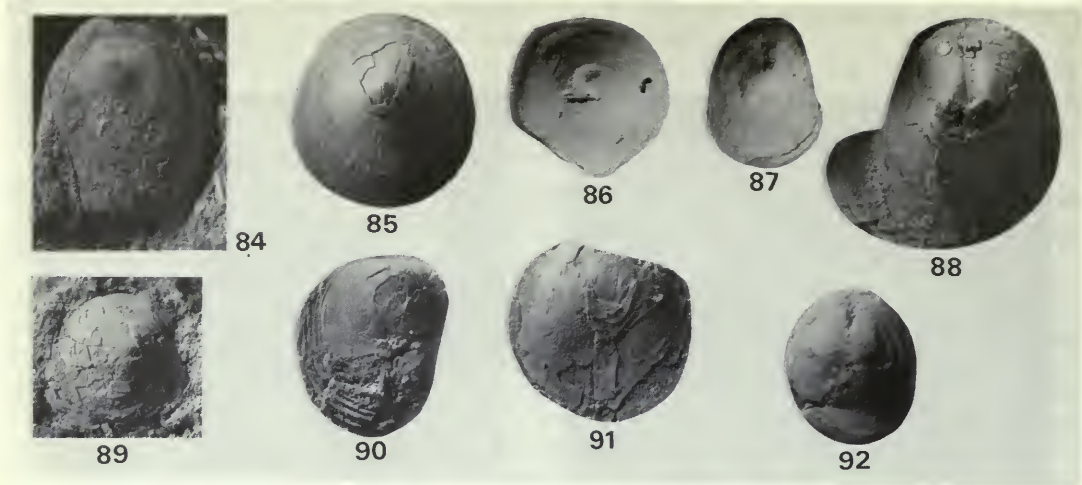

Figs 84–92 *Orbiculoidea ovata* sp. nov., brachial valves: 84 = BB 72274, ×2·5, 85 = **holotype** BB 72273, ×2·7, 86 = BB 24949, ×2; pedicle valves: 87 = BB 72275, ×3, 88 = BB 31260, ×2·7. *Orbiculoidea* sp.: 89 = brachial valve BB 24948, ×3·3. *Schizotreta* sp. 1: 92 = pedicle valve BB 24950, ×8·5. *Schizotreta* sp. 2, brachial valves: 90 = BB 72276, ×3·5, 91 = BB 72277, ×3.

Dorsal interior with very indistinct muscle impressions anterior of apex and from which two indistinct pallial tracks extend anterolaterally.

Ventral interior smooth and with pedicle groove extending posteriorly from the umbo for 31% (values for 2 valves 31% each) of the length of the valve.

DIMENSIONS.	length	width
Exterior of brachial valve, BB 72273, holotype	9·8	9·2
Exterior of brachial valve, BB 72274	8·7	8·6
Exterior of pedicle valve, BB 72275	6·5	5·2
Partially exfoliated pedicle valve, BB 31260	11·5	10·0
Internal mould of brachial valve, BB 24949	11·5	11·0

HORIZON AND LOCALITIES. BB 72273–4 from type locality, loc. 44. Paratypes BB 24949 from loc. 47, BB 72275 from loc. 48 and BB 31260 from well excavation at Plaish. Also recorded from locs 35 and 43.

Orbiculoidea sp.

Fig. 89

There is a partially exfoliated brachial valve in the BM(NH) collection (BB 24948) from calcareous sediments of the Acton Scott Formation at Batch Gutter in the Onny Valley (SO 4245 8538). The valve, which was 6·0 mm long, 5·7 mm wide and 1·6 mm deep, was subcircular in outline with the beak situated 2·2 mm forward of the posterior margin. The transverse profile was evenly convex and the external surface ornamented by two sets of fila, one very fine and on average 2 mm apart and the other intercalated and very impersistent. *Orbiculoidea* occurs sparsely in Upper Caradoc rocks of east Salop. Most specimens belong to the new species *O. ovata*, which differs from the present *Orbiculoidea* sp. only in details of the ornament.

Genus *SCHIZOTRETA* Kutorga, 1848

Schizotreta sp. 1

Fig. 92

An internal mould of a pedicle valve in the BM(NH) collection (BB 24950) is the sole representative of *Schizotreta* sp. 1. It is from the Onny Shale Formation of the Onny river cliff, loc. 51. The valve, which was approximately 3·1 mm long, 2·2 mm wide and 0·6 mm deep, was oval in outline with the low depressed beak situated 1·0 mm forward of the truncated posterior margin. The transverse profile was evenly convex and the external surface ornamented by coarse fila.

Schizotreta sp. 2
Figs 90, 91

Two partially exfoliated brachial valves (BB 72276–7) from loc. 44 of the Acton Scott Formation are the only representatives of *Schizotreta* sp. 2 from the east Salop Upper Caradoc. BB 72276, 5·5 mm long, 5·3 mm wide and 1·1 mm deep, is suboval in outline with a rounded anterior margin, parallel lateral margins and a truncated posterior with a slightly overhanging marginal beak; its internal features are unknown. The shell surface is ornamented by very coarse concentric ridges. BB 72277a, b, a fragmentary specimen, is 7 mm wide and over 7·5 mm long and 1·5 mm deep.

DISCUSSION. It is considered unlikely that *Schizotreta* sp. 1 and sp. 2 are conspecific, because of their difference in ornament. In the development of strong coarse concentric ridges, submarginal beak and truncated posterior margin *Schizotreta* sp. 2 closely resembles the older *S. corrugata* Cooper from the Porterfield Pratt Ferry Formation of Alabama (Cooper 1956 : 277).

Class **ARTICULATA** Huxley, 1869
Order **ORTHIDA** Schuchert & Cooper, 1932
Suborder **ORTHIDINA** Schuchert & Cooper, 1932
Superfamily **ORTHACEA** Woodward, 1852
Family **ORTHIDAE** Woodward, 1852
Subfamily **PRODUCTORTHINAE** Schuchert & Cooper, 1931

Genus ***NICOLELLA*** Reed, 1917

Nicolella actoniae (J. de C. Sowerby)

1839 *Orthis actoniae* J. de C. Sowerby *in* Murchison : 639; pl. 20, fig. 16 (left); *non* pl. 20, fig. 16 (right).
1963 *Nicolella actoniae* (J. de C. Sowerby); Williams : 352–356; pl. 1, figs 15–19.
cf. 1974 *Nicolella* cf. *actoniae* (J. de C. Sowerby); Williams : 57–58; pl. 9, figs 1–6.
cf. 1977 *Nicolella* cf. *actoniae* (J. de C. Sowerby); Mitchell : 31–32; pl. 3, figs 14–20.

Williams (1963) has redescribed and figured *N. actoniae*, and his work will not be duplicated here. He records the species definitely from loc. 45, where in my collections it is rare, and possibly from loc. 47, where I have not found it. It also occurs at loc. 43 and abundantly at loc. 44. All these localities are in the Acton Scott Formation.

Family **DOLERORTHIDAE** Öpik, 1934

Genus ***DOLERORTHIS*** Schuchert & Cooper, 1931

Dolerorthis virgata (J. de C. Sowerby)
Figs 93–105

1839 *Orthis virgata* J. de C. Sowerby *in* Murchison : 639; pl. 20, fig. 15.
1869 *Orthis calligramma* var. *virgata* J. de C. Sowerby; Davidson : 240 *pars*; pl. 35, figs 23, 24, *non* figs 1–22.
1869 *Orthis virgata* J. de C. Sowerby; Davidson : 240; pl. 37, fig. 2.
1958 *Dolerorthis duftonensis* (Reed); Dean : pl. 25, fig. 1.
1978 *Dolerorthis virgata* (J. de C. Sowerby); Cocks : 45.

DESCRIPTION. Subcircular to subquadrate, unequally bioconvex *Dolerorthis* with rectangular cardinal margins; brachial valve 76% as long as wide, evenly convex, non-sulcate and 14% as deep as long; dorsal interarea anacline, notothyrium open; pedicle valve 84% as long as wide, evenly convex and 24% as deep as long; long apscaline interarea, delthyrium open; ornamentation costellate commonly with two ribs per mm, 10 mm anteromedially of the dorsal umbo, cancellated by fine concentric lamellae.

Ventral muscle scar subpentagonal, extending anteriorly for 35% of the length of the valve and 30% as wide as the valve is long; lanceolate adductor scar not surrounded by diductor tracks; teeth strong, supported by short subparallel dental lamellae extending anteriorly of umbo for 17% of the valve length.

Dorsal interior with simple ridge-like cardinal process; brachiophores simple, stout, widely divergent with their bases extending anteriorly of the dorsal umbo for 16% of the valve length and splaying laterally for 33% of the valve length; dorsal adductor field quadripartite with posterior scars larger than anterior and extending anteriorly for 50% of the length of the valve.

MATERIAL. Lectotype (selected Cocks 1978: 45) GSM Geol. Soc. Coll. 6904 (Fig. 95), length 17·9 mm, width 22·2 mm, from calcareous sandstones at Acton Scott, possibly locs 47 or 48. Other material from loc. 12, coll. O18 (e.g. Figs 93, 102, BB 72395, length 19·8 mm and width 25·0 mm, and Fig. 94, BB 72396, length 14·5 mm and width 19·0 mm), O112 (e.g. Fig. 100, BB 72397, length 24 mm and width 26·0 mm, and Fig. 105, BB 72398, length 9·8 mm and width 13·8 mm) and O19 (e.g. Fig. 97, BB 72399 and Fig. 104, BB 72400); also loc. 27, coll. M20 (e.g. Fig. 98, BB 72401, Fig. 103, BB 72402, Fig. 99, BB 72403 and Fig. 96, BB 72404); also loc. 40, coll O103 (e.g. Fig. 101, BB 72405) and locs 10, 11, 17, 32, 41 and 48.

DISCUSSION. *Dolerorthis* occurs sparingly in the Upper Caradoc, but the small samples have been combined to obtain the statistics in Tables 16–25. The sample from the Alternata Limestone and Glynboro Member does not differ in terms of the known bivariate characteristics from the Crosspipes Member and Acton Scott Formation sample, although a larger collection may show the later sample to consist of slightly more coarsely-ribbed individuals. However, such a minor difference is not taxonomically important, so all Upper Caradoc *Dolerorthis* are included in *D. virgata*.

D. virgata differs from *D. duftonensis prolixa* Williams in a number of characters, namely in having a relatively longer brachial valve ($P<0·01$), a slower increase in depth of the brachial valve ($P<0·02$), relatively longer dorsal cardinalia ($P<0·01$) and a slower increase in length of the dorsal muscle field($P<0·01$). *D. virgata* does not differ in any of its statistical data from those given by Williams (1963 : 60–61) for *D. duftonensis*. However, there may be significant differences between the two as the former species appears to have a shallower pedicle valve and a longer ventral muscle field. *D. duftonensis* could be a synonym of *D. virgata*, but until more is known about the variation of *D. duftonensis* the two species are kept separate.

Family **DINORTHIDAE** Schuchert & Cooper, 1931

Genus ***DINORTHIS*** Hall & Clarke, 1892

Dinorthis sp.
Figs 106, 111

DESCRIPTION. Subquadrate, dorsibiconvex *Dinorthis* with a brachial valve 76% as long as wide and 26% as deep as long; pedicle valve weakly convex with slightly raised umbonal region, and

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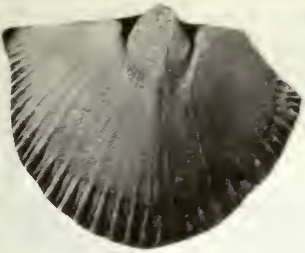
Figs 93–111 *Dolerorthis virgata* (J. de C. Sowerby), internal moulds of pedicle valves: 93 = BB 72395a, ×1·6, 94 = BB 72396, ×2·6, 95 = lectotype, GSM 6904, ×2, 96 = BB 72404, ×1·1, 97 = BB 72399, ×1·2, 99 = BB 72403, ×1·1; external mould of pedicle valve: 102 = BB 72395b, ×2·5; internal moulds of brachial valves: 98 = BB 72401, ×1·3, 100 = BB 72397, ×1·5, 101 = BB 72405, ×2, 103 = BB 72402, ×1·2, 104 = BB 72400, ×2, 105 = BB 72398, ×2. *Dinorthis* sp., internal mould of pedicle valve: 106 = BB 72407, ×1·5; internal mould of brachial valve: 111 = BB 72406, ×0·8. *Platystrophia* sp. 1, internal mould of pedicle valve: 107 = BB 72394, ×1; internal moulds of brachial valves: 108 = BB 72368, ×2, 109 = BB 72367, ×1·2. *Platystrophia* sp. 2, internal mould of brachial valve: 110 = BB 72369, ×3·5.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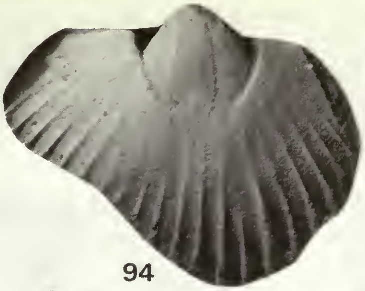
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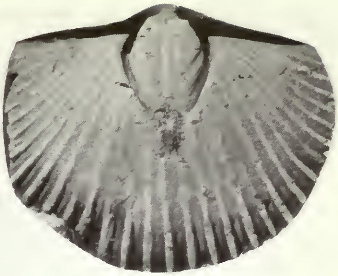
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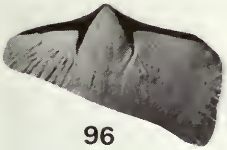
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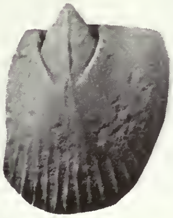
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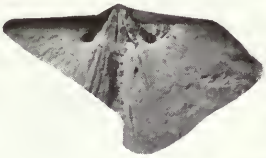
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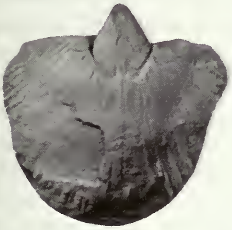
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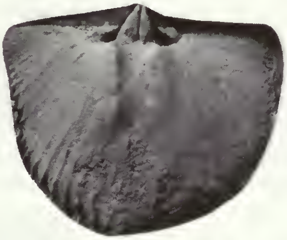
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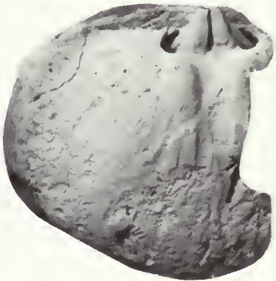
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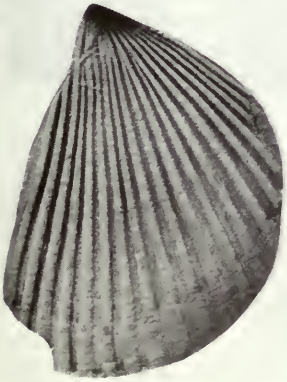
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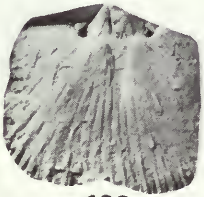
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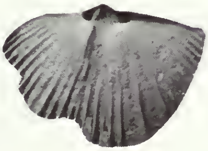
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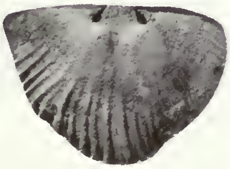
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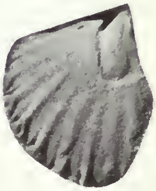
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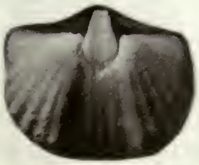
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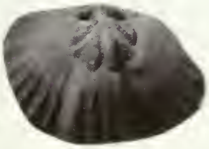
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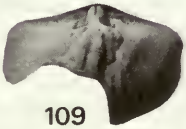
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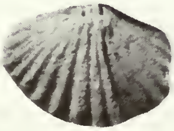
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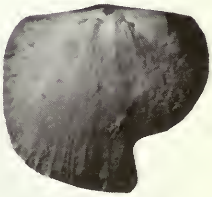
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73% as long as wide; ventral interarea apscaline, dorsal interarea orthocline; radial ornamentation of strong costae; ventral muscle scar elongately subrectangular, 40% as long as the valve and 28% as wide as the valve is long; teeth blunt and supported by short dental lamellae extending anteriorly for 15% of the valve length; cardinal process differentiated into short stout shaft and expanded myophore; brachiophores stout, unsupported and extending forward of dorsal umbo for 15% the length of the valve and splaying laterally for 29% the length of the valve; dorsal adductor field suboval, weakly impressed and extending anterior of dorsal umbo for about half the length of the valve.

HORIZON AND LOCALITIES. BB 72406, brachial valve (length 28·7 mm, width 38·0 mm) from loc. 29, BB 72407, pedicle valve (length 15·4 mm, width 21·2 mm) from loc. 13. Also recorded from locs 15, 18, 30 and 32.

Family **PLECTORTHIDAE** Schuchert & Le Vene, 1929
Subfamily **PLATYSTROPHIINAE** Schuchert & Le Vene, 1929

Genus ***PLATYSTROPHIA*** King, 1850

Platystrophia sp. 1
Figs 107–109

The only specimens, from the Crosspipes Member, are an incomplete complementary external and internal mould of a brachial valve (BB 72367; loc. 24, colln WFT2), a complete internal mould (BB 72368; loc. 24, colln WFT1) and an internal mould of a pedicle valve (BB 72394; loc. 27, colln M6). The brachial valves were 68% as long as wide and 33% as deep as long with a well-defined slightly rounded fold about 34% as wide as the valve. The radial ornamentation consisted of four costae on the fold and five on each lateral slope, with a wavelength of 1 mm, 5 mm anteromedially of the dorsal umbo. Cardinal process ridge-like; short, thick, slightly divergent brachiophores bound wide notothyrium, extending anteriorly for 17% of the length of the valve and splaying laterally for 34% of the valve length; dorsal adductor scars strongly impressed, quadripartite, extending anteriorly for 49% the length of the valve on either side of a low thin median ridge. The pedicle valve was 25 mm wide, 20·2 mm long and 6 mm deep, with an elongately oval, subtriangular muscle field 32% as long as the valve and 18% as wide as the valve is long; small thick pedicle callist; teeth stout, supported by short dental plates extending anteriorly for 16% the length of the valve.

Platystrophia sp. 2
Fig. 110

The only specimen, from the Acton Scott Formation, is an internal mould of a brachial valve (BB 72369; loc. 43, colln CP3). The valve, which was 4·7 mm long, 6·7 mm wide and 1·7 mm deep,

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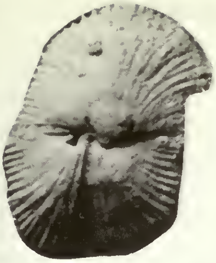
Figs 112–144 *Rhactorthis grandis* sp. nov., internal moulds of pedicle valves: 113 = BB 72349, ×2, 114 = BB 72351, ×3·7, 115 = BB 72353, ×3, 116 = BB 72352, ×3, 117 = BB 72357, ×4, 118 = BB 72354a, ×3·3, 120 = BB 72350, ×4; partially conjoined valves, **holotype**: 112 = BB 72348, ×4; external mould of pedicle valve: 119 = BB 72354b, ×3·3; internal and external moulds of brachial valves: 121 = BB 72359a, ×2·5, 122 = BB 72359b, ×2·5, 123 = BB 72362, ×2·3, 124 = BB 72361b, ×3, 125 = BB 72361a, ×3, 126 = BB 72358, ×3·2, 127 = BB 72360, ×2·7, 128 = BB 72356, ×5, 129 = BB 72355, ×5·3, 130 = BB 72363, ×3. *Rhactorthis actoniae* sp. nov., **holotype,** internal mould of pedicle valve: 131 = BB 72364, ×1·5; internal and external moulds of brachial valves: 132 = BB 72365, ×3·3, 133 = BB 72366a, ×2, 134 = BB 72366b, ×2·2. *Rhactorthis* cf. *crassa* Williams, internal and external moulds of pedicle valves: 135 = BB 72381, ×3·2, 136 = BB 72380, ×2, 137 = BB 72382, ×6·5, 138 = BB 72379a, ×4·5, 139 = BB 72379b, ×4·5; internal moulds of brachial valves: 140 = BB 72377, ×5, 141 = BB 72376, ×2, 142 = BB 72378, ×5·5. *Gelidorthis* sp., internal mould of pedicle valve: 143 = BB 72373, ×5. Plectorthid gen. et sp. indet., internal mould of pedicle valve: 144 = BB 72374, ×3.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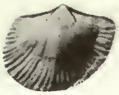
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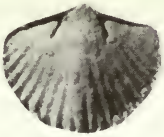
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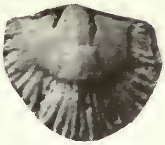
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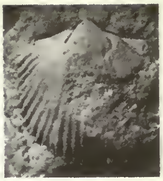
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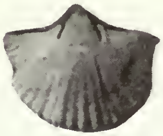
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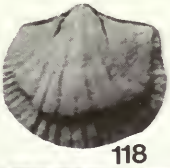
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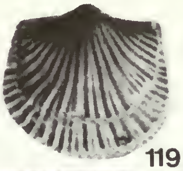
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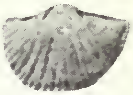
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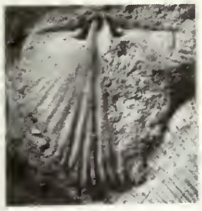
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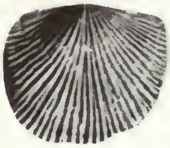
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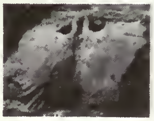
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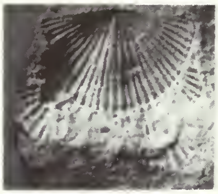
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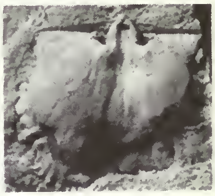
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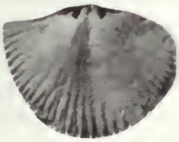
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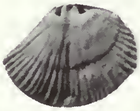
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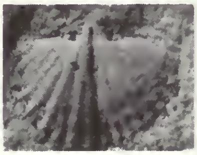
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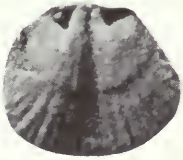
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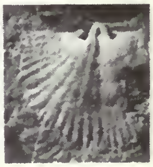
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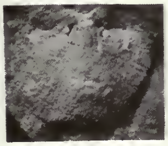
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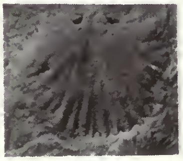
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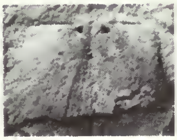
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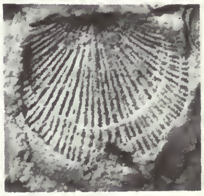
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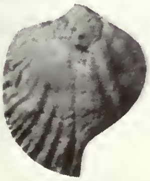
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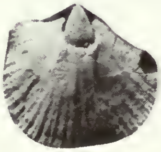
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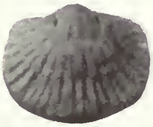
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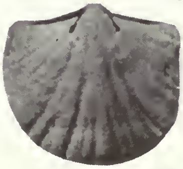
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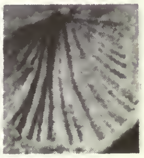
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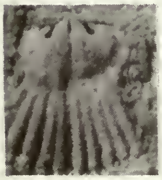
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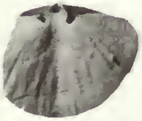
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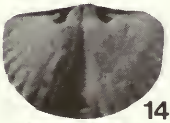
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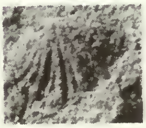
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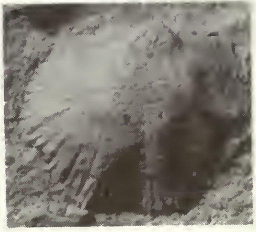
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had a poorly-developed rounded sulcus 2·5 mm wide. Radial ornamentation of three costae on the fold and seven on each lateral slope. Cardinal process ridge-like, brachiophore bases subparallel and extending anteriorly for 13% the length of the valve; fulcral plates present.

Subfamily **RHACTORTHINAE** Williams, 1963

Genus ***RHACTORTHIS*** Williams, 1963

TYPE SPECIES. *Rhactorthis crassa* Williams, 1963 by original designation.

Rhactorthis actoniae sp. nov.

Figs 131–134

DESCRIPTION. Subcircular unequally biconvex *Rhactorthis* with sulcate brachial valve, 80% as wide as long and 20% as deep as long; evenly convex pedicle valve 83% as wide as long and 25% as deep as long, pedicle interarea slightly curved apscaline, brachial interarea straight anacline; delthyrium and notothyrium open; radial ornamentation commonly of five costellae (measured on 4 valves) per mm, 2 mm anteromedially of the dorsal umbo, commonly arising by dichotomous branching; disruptive growth lines occasionally present.

Ventral muscle scar subpentagonal and extending anteriorly for 30% the length of the valve and 33% as wide as the valve is long; diductor scar does not surround median adductor scar; teeth small, supported by receding dental lamellae and extending anteriorly for 18% the length of the valve.

Dorsal interior with very shallow median ridge, at posterior end of which arises continuous shaft of cardinal process which is crenulated posteriorly, fills notothyrium and projects slightly beyond hinge line; brachiophores very short, divergent and extending anteriorly for 17% the length of the valve, with delicate convergent bases which curve laterally parallel to hinge line for 34% the length of the valve; adductor scars very weakly impressed, elongately oval and extending anteriorly for 44% the length of the valve.

NAME. Referring to the locality near Acton Scott.

DIMENSIONS.	length	width
Internal mould of pedicle valve, BB 72364, holotype	6·5	12·0
Internal mould of brachial valve, BB 72365	5·1	6·0
External and internal moulds of brachial valve, BB 72366a, b	9·6	10·7

HORIZON AND LOCALITIES. Type material from loc. 47, colln CF3, the only locality from which the species has been recovered.

DISCUSSION. See under *R. grandis*, p. 239.

Rhactorthis cf. ***crassa*** Williams

Figs 135–142

cf. 1963 *Rhactorthis crassa* Williams : 372–375; pl. 4, figs 1–6.

DESCRIPTION. Subcircular to subquadrate, moderately biconvex *Rhactorthis* with weakly sulcate brachial valve 82% as wide as long and 25% as deep as long, lateral slopes moderately strong, evenly convex with shallow rounded sulcus originating at umbo; pedicle valve moderately convex, 82% as wide as long and 32% as deep as long; ventral interarea apscaline, dorsal interarea anacline; delthyrium and notothyrium open; radial ornamentation of five to eight low angular costellae per mm, 2 mm anteromedially of the dorsal umbo, arising by dichotomous branching; internal branching common, externals not observed; concentric lamellae common, but no major disruption by growth lines.

Ventral muscle scar elongately subpentagonal and extending anteriorly for 32% of the valve length and 28% as wide as the valve is long; adductor scar not surrounded anteriorly by diductor impressions; teeth small and supported by short divergent dental lamellae extending anteriorly for 20% of the valve length; dental lamellae continued along sides of muscle field as shell ridges and meet anteromedially to surround muscle field completely.

Dorsal interior with wide rounded median ridge; cardinal process shaft broad and continuous with posterior end of median ridge; myophore crenulated, completely filling notothyrium and extending slightly beyond hinge line; subparallel to divergent short, stout brachiophores extending anteriorly for 17% the length of the valve, with convergent bases which sometimes curve laterally for 43% of the length of the valve; sockets small and deep; adductor scars very weakly impressed, situated on either side of median ridge and extending anteriorly for 45% of the valve length.

MATERIAL AND LOCALITIES. Loc. 43, colln CP4 (e.g. Fig. 141, BB 72376, length 8·5 mm, width 9·6 mm), colln CP1 (e.g. Fig. 136, BB 72380, length 9·0 mm, width 10·0 mm and Fig. 142, BB 72378) and CP2 (e.g. Fig. 135, BB 72381). Loc. 45, colln AS4 (e.g. Fig. 140, BB 72377, length 3·2 mm, width 4·0 mm and Figs 138–9, BB 72379, length 4·5 mm, width 5·2 mm) and colln AS6 (e.g. Fig. 137, BB 72382, length 2·6 mm and width 3·1 mm.)

Rhactorthis grandis sp. nov.

Figs 112–130

DESCRIPTION. Subcircular, strongly biconvex *Rhactorthis* with strongly sulcate brachial valve 78% as wide as long and 23% as deep as long, lateral slopes strong, evenly convex and with deep, persistent, rounded sulcus originating at umbo; pedicle valve strongly convex, sometimes strongly carinate, 84% as wide as long and 33% as deep as long; apscaline ventral interarea over one-fifth as long as the pedicle valve; anacline dorsal interarea over one-eighth as long as dorsal valve; delthyrium and notothyrium open; radial ornamentation commonly of five or six costellae per mm, 2 mm anteromedially of the dorsal ubmo, arising by dichotomous branching, externals rarely developed, internals common; growth lines lamellose with occasional large disruptive growth lines.

Ventral muscle scar rounded subpentagonal and extending anteriorly for 31% the length of the valve and 34% as wide as the valve is long; wide adductor scar not surrounded anteriorly by diductor impressions; teeth small and supported by very short, delicate dental lamellae extending anteriorly for 19% the length of the valve.

Dorsal interior with well-developed ridge posteriorly; wide ridge-like cardinal process continuous with median ridge and posteriorly crenulated, filling notothyrium, projecting slightly beyond hinge line; divergent, short brachiophores extending anteriorly for 16% the length of the brachial valve and with convergent bases which curve laterally away from median plane, for 37% the length of the valve, parallel with hinge line to define small deep sockets; adductor scars very weakly impressed, situated on either side of median ridge, immediately anterior of the brachiophores and extending anteriorly for 48% the length of the valve.

DIMENSIONS.	length	width
BB 72348, holotype, pedicle valve (Fig. 112)	5·0	5·8
holotype, brachial valve	4·3	5·8
BB 72349, pedicle internal mould (Fig. 113)	5·8	8·2
BB 72350, pedicle internal mould (Fig. 120)	3·2	4·5
BB 72352, pedicle internal mould (Fig. 116)	6·5	6·6
BB 72355, brachial external and internal mould (Fig. 129)	3·8	4·5
BB 72363, brachial external and internal mould (Fig. 130)	5·9	7·0
BB 72359, brachial external and internal mould (Fig. 121)	7·6	8·6

LOCALITIES. BB 72348–53 and BB 72359–62 from loc. 25, colln WFT7; BB 72354 from loc. 25, colln WFT9; BB 72355–8 and BB 72363 from loc. 28, colln M11. Also recorded from locs 22 and 33.

DISCUSSION. Four samples of *Rhactorthis* have been assessed statistically, and the data set out in Tables 26–35. *Rhactorthis* from locs 25 (A in tables) and 28 (B in tables) in the *O. reuschi* Zone of the Crosspipes Member do not differ in their bivariate characteristics and consequently are treated as representing a single new species, *R. grandis.*

R. actoniae differs from *R. grandis* from loc. 25 in having a slower increase in depth of the pedicle valve ($P < 0{\cdot}01$) and in a relatively narrower ventral muscle field ($P < 0{\cdot}05$). *R. actoniae* differs from *R. grandis* from loc. 28 in having a relatively narrower ventral muscle field ($P < 0{\cdot}01$) and a slower increase in length of the dorsal muscle field ($P < 0{\cdot}05$). Further, the pedicle valves of *R. actoniae* are moderately evenly convex whereas those of *R. grandis* are often carinate, resembling *R. melmerbiensis* (Reed) from the Dufton shales (Reed 1910 : pl. 23), but not as deep (Williams 1963 : 375). The two species further differ in the configuration of the dorsal cardinalia, with *R. melmerbiensis* apparently possessing shorter brachiophores whose bases do not splay to run parallel to the hinge line.

R. crassa Williams, the type species of the genus, from the Gelli-grîn Calcareous Ashes (Longvillian), differs from *R. grandis* in having relatively wider dorsal cardinalia ($P < 0{\cdot}001$ with loc. 25 and $P < 0{\cdot}01$ with loc. 28 *R. grandis*). Further, *R. grandis* has a carinate pedicle valve. *R. grandis* has fine radial ornamentation with counts of 5, 6 and 7 ribs per mm, 2 mm anteromedially of the dorsal umbones of 8, 8 and 1 specimens respectively, figures which are comparable to the costae counts derived from the published photographs of *R. crassa* (Williams 1963 : pl. 4) but not consistent with the species description (see Williams 1963 : 374). The brachial valve of *R. grandis* has $3\bar{a}$ arising earlier than $1\bar{a}$ and earlier than $2\bar{a}$ in 4 out of 5 and 5 out of 5 specimens respectively; these proportions are significantly different from those in *R. crassa* ($P < 0{\cdot}2$ and $P < 0{\cdot}02$ respectively).

R. cf. *crassa* differs from *R. grandis* in the faster relative increase in length of the dorsal cardinalia ($P < 0{\cdot}05$–$0{\cdot}02$) and length of the adductor scar ($P < 0{\cdot}05$), relatively shallow pedicle valve ($P < 0{\cdot}05$) and relatively longer pedicle muscle field ($P < 0{\cdot}02$). From *R. actoniae*, *R.* cf. *crassa* differs in having a relatively longer brachial valve ($P < 0{\cdot}05$) and relatively shorter dorsal muscle field ($P < 0{\cdot}05$). Further, the ribbing of *R.* cf. *crassa* is fine, having 5, 6, 7 and 8 costellae per mm, 2 mm anteromedially of the dorsal umbo on 2, 1, 1 and 1 shells respectively. This distribution is significantly finer than in *R. grandis* ($P < 0{\cdot}03$), and in *R. actoniae* ($P < 0{\cdot}05$) which has 4 costellae at the appropriate distance from the dorsal umbo on 4 shells.

R. cf. *crassa* differs from *R. crassa* only in having a significantly ($P < 0{\cdot}02$) faster increase in length of the ventral muscle field, This difference is not sufficient to warrant the erection of a new species, so the specimens of *Rhactorthis* from the Actonian siltstones of locs 43 and 45 are referred to *R.* cf. *crassa.*

Subfamily **PLECTORTHINAE** Schuchert & Le Vene, 1929

Genus ***GELIDORTHIS*** Havlíček, 1971

Gelidorthis sp.

Fig. 143

A complete internal and external mould of a very small pedicle valve (BB 72373) from loc. 48, colln ASHI, is provisionally assigned to *Gelidorthis*. The valve, which was 2·3 mm long and 3·2 mm

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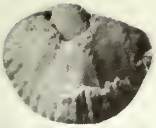
Figs 145–180 *Skenidioides* cf. *costatus* Cooper, internal moulds of pedicle valves: 145 = BB 72388, ×2·5, 146 = BB 72391, ×4·6, 147 = BB 72390, ×5·4, 148 = BB 72393, ×4, 149 = BB 72389, ×3, 150 = BB 72392, ×4·3; internal and external moulds of brachial valves: 151 = BB 72384a, ×3·5, 152 = BB 72384b, ×3·5, 153 = BB 72383a, ×4, 154 = BB 72383, ×4, 155 = BB 72386, ×5, 156 = BB 72385b, ×5·7, 157 = BB 72385a, ×5·7, 158 = BB 72387b, ×3·4, 159 = BB 72387a, ×3·4. ? *Drabovia* sp., internal mould of brachial valve: 160 = BB 72372, ×1·7. *Destombesium* sp., internal mould of brachial valve: 161 = BB 72375, ×2. *Dalmanella multiplicata multiplicata* (Bancroft), internal and external moulds of brachial valves: 162 = lectotype BB 9379, ×1·5, 163 = BB 72308a, ×1·4, 164 = BB 72308b, ×1·5, 165 = BB 72296b, ×1·8, 166 = BB 72296a, ×2, 167 = BB 72297, ×2, 168 = BB 72295a, ×2·1, 169 = BB 72295b, ×2, 170 = BB 72309, ×2, 178 = BB 72304, ×1·3, 179 = BB 72305a, ×2, 180 = BB 72305b, ×1·3; internal moulds of pedicle valves: 171 = BB 72292, ×2, 172 = BB 72293, ×1·8, 173 = BB 72307, ×3, 174 = BB 72294, ×2, 175 = BB 72306, ×2·7, 176 = BB 72303, ×1·8, 177 = BB 72302, ×1·3.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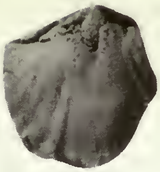
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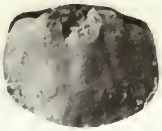
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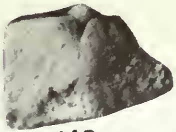
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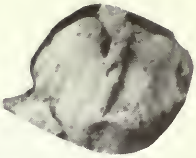
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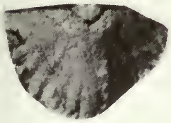
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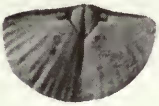
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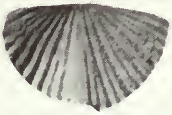
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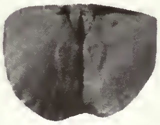
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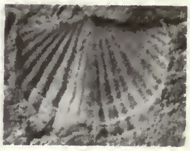
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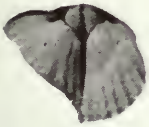
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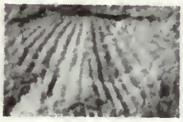
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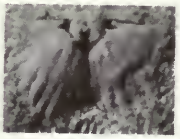
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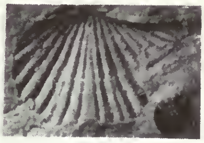
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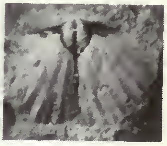
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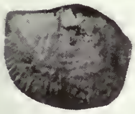
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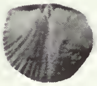
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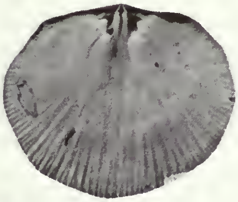
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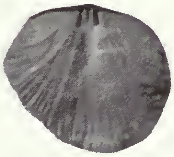
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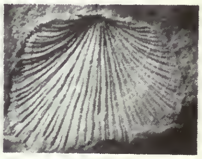
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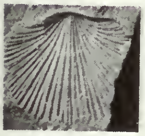
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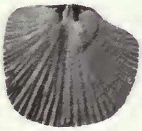
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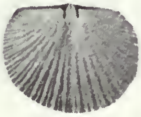
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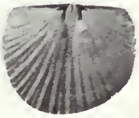
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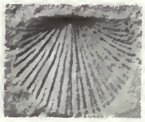
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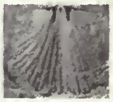
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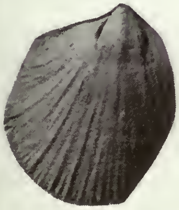
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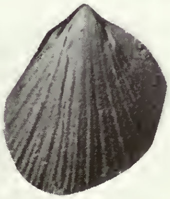
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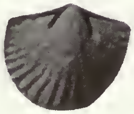
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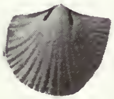
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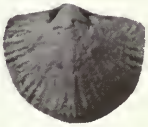
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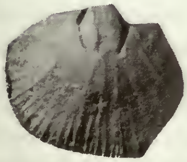
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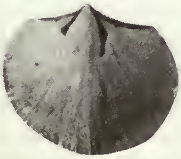
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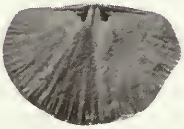
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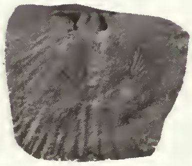
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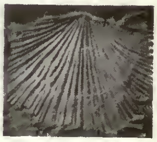
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wide, was evenly convex and very shallow. Radial ornamentation of relatively coarse angular ribs; obscure ventral muscle field; dental plates very short and subparallel.

Plectorthid gen. et sp. indet.
Fig. 144

A complete pedicle valve (BB 72374) from loc. 44, colln OA32, is a plectorthid. The subcircular valve was 6·8 mm long, 10·0 mm wide and 2·3 mm deep. The external surface was ornamented by branching hollow costellae. The teeth were small and supported by short, widely-divergent dental lamellae extending anteriorly for 12% of the length of the valve; muscle scar rounded and subpentagonal, extending anteriorly for 21% of the length of the valve and 30% as wide as the valve is long.

Family **SKENIDIIDAE** Kozłowski, 1929

Genus ***SKENIDIOIDES*** Schuchert & Cooper, 1931

Skenidioides cf. ***costatus*** Cooper
Figs 145–159

cf. 1956 *Skenidioides* cf. *costatus* Cooper : 493–494; pl. 97, figs 33–48.
cf. 1962 *Skenidioides* cf. *costatus* Cooper; Williams : 126–127; pl. 11, figs 24–27, 52.
cf. 1963 *Skenidioides* cf. *costatus* Cooper; Williams : 375–377; pl. 4, figs 7–14.
cf. 1974 *Skenidioides* cf. *costatus* Cooper; Williams: 82–83; pl. 13, figs 14–16; pl. 14, figs 1–3.

DESCRIPTION. Ventribiconvex, oval *Skenidioides* with a pedicle valve 74% as long as wide and 26% as deep as long; brachial valve very gently convex, 70% as long as wide and with a sharp median sulcus originating at umbo; radial ornamentation costellate with 7 or 8 rounded costae occupying each lateral slope and between 3 and 5 costae per mm, 2 mm anteromedially of the dorsal umbo; internal branching common, external absent.

Ventral interior with free spondylium 26% as deep as the length of the valve.

Dorsal interior with thin ridge-like shaft of cardinal process continuous posteriorly with thin high median septum which is 81% as long as the valve; brachiophore bases converging onto dorsal septum and extending anteriorly for 37% of the valve length and 52% as wide as the valve is long; adductor muscle field impressed about median septum and extending anteriorly for nearly three-quarters of the valve length.

MATERIAL AND LOCALITIES. Loc. 27, colln M2 (e.g. Fig. 147, BB 72390, length 3·8 mm, width 5·0 mm). Loc. 43, colln CP2 (e.g. Fig. 145, BB 72388, length 6·2 mm, width 8·0 mm and Fig. 149, BB 72389). Loc. 44, colln OA29 (e.g. Figs 151–2, BB 72384, length 3·9 mm, width 5·8 mm, and Figs 156–7, BB 72385, length 2·5 mm, width 3·5 mm). Loc. 45, colln AS4 (e.g. Figs 153–4, BB 72383, length 4·0 mm, width 5·2 mm) and colln OA30 (e.g. Fig. 155, BB 72386). Loc. 48, colln ASH1 (e.g. Fig. 148, BB 72393, and Fig. 150, BB 72392, length 3·5 mm, width 5·4 mm) and colln ASH2 (e.g. Figs 158–9, BB 72387, and Fig. 146, BB 72391).

DISCUSSION. *Skenidioides* occurs sporadically throughout the Actonian. Two small samples, one from calcareous sandstones (loc. 48) and the other from siltstones (locs 43–5), have been statistically analysed (see Tables 36–42). They do not differ from each other in bivariate characteristics, or from *S.* cf. *costatus* (see Williams 1963) found in the Gelli-grîn Calcareous Ashes of north Wales. The sample from the siltstone has similar ribbing to *S.* cf. *costatus* from the Gelli-grîn Calcareous Ashes but it may be slightly finer than in the *Skenidioides* from the calcareous sandstones, in which one dorsal valve had only 3 ribs at the fixed distance from the umbo as opposed to 4 or 5. However, this possible difference is not considered important enough to warrant taxonomic recognition and so all *Skenidioides* from the Actonian are recorded as *S.* cf. *costatus.*

Superfamily **ENTELETACEA** Waagen, 1884
Family **SCHIZOPHORIIDAE** Schuchert & Le Vene, 1929
Subfamily **DRABOVIINAE** Havlíček, 1950

Genus ***DESTOMBESIUM*** Havlíček, 1970

Destombesium sp.
Fig. 161

An internal mould of a brachial valve (BB 72375) from loc. 25, colln WFT8 is provisionally assigned to *Destombesium*. The subcircular valve was 6·3 mm long and 7 mm wide, with a well-developed median sulcus, and a short, planar, anacline interarea. Valve interior with very thin undifferentiated cardinal process filling narrow notothyrium; brachiophores thin, subparallel and extending anteriorly for 16% of the valve length and splayed laterally for 25% of the valve length; brachiophore bases convergent; fulcral plates present; adductor muscle scars not impressed. Although the single specimen cannot be statistically compared with any described species of the genus, it is similar to *D. zagoraensis* from the Ashgill of Morocco (see Havlíček 1971 : pl. 15).

Genus ***DRABOVIA*** Havlíček, 1950

? ***Drabovia*** sp.
Fig. 160

The internal mould (BB 72372) of a brachial valve about 8 mm long and 10 mm wide from the Acton Scott Beds (loc. 46) is questionably assigned to *Drabovia*. The valve is subcircular in outline and about one-quarter as deep as long and with a shallow median sulcus. Interarea short, slightly curved, anacline, cardinal process with small, bulbous, crenulated myophore and long thin shaft; brachiophores short with convergent bases and about one-fifth as long as the valve and splaying laterally for one-quarter the valve width, sockets defined by fulcral plates; muscle scar unknown.

Family **DALMANELLIDAE** Schuchert, 1913

Genus ***DALMANELLA*** Hall & Clarke, 1892

Dalmanella multiplicata multiplicata (Bancroft)
Figs 162–185

1928a *Wattsella multiplicata* Bancroft : 58–59; pl. 2, figs 11–14.

Description. Typically rounded ventribiconvex *Dalmanella*, with an evenly, weakly convex brachial valve 80% as long as wide and with a very shallow median sulcus; pedicle valve 85% as long as wide and 26% as deep as the valve is long; delthyrium and notothyrium open, pedicle callist inconspicuous, ventral interarea curved apscaline, longer than anacline dorsal interarea; radial ornamentation of costellae commonly 4 to 6 per mm, 2 mm anteromedially of the dorsal umbo; rib branching complex with both external and internal secondaries freely developed except on the first primary which only has internals.

Ventral muscle field bilobed, with diductor scars extending anteriorly for 32% of the length of the pedicle valve but not surrounding the median adductor muscle field; diductor scars 32% as wide as the pedicle valve is long; teeth small, with shallow crural fossettes variably developed, and supported by dental plates, extending anteriorly for 21% of the length of the pedicle valve, along the sides of the diductor muscle area as a pair of strong, slightly convergent ridges.

Dorsal interior with cardinal process consisting of thin linear shaft with small, expanded, rounded myophore which is crenulated; brachiophores short, strong, divergent, with parallel to subparallel bases flanking well-developed notothyrial platform and extending anteriorly for 20% of the length of the brachial valve and splaying laterally for 31% of the valve length; elongately suboval adductor scars poorly differentiated, often obscured by ribbing, situated on either side of low median ridge and extending anteriorly for 50% of the length of the brachial valve.

MATERIAL AND LOCALITIES. Lectotype (selected Cocks 1978 : 62) Fig. 162, BB 9379, length 16·0 mm, width 20·7 mm; also Figs 165–9 and 171, 172, 174, BB 72292–7, all from loc. 18, new material colln x. Figs 176–180, BB 72302–5, from loc. 19, colln CL3. Figs 181–5, BB 72310–3, from loc. 27, colln M1. Figs 163–4, BB 72308, length 13·9 mm, width 16·0 mm; Fig. 170, BB 72309, length 5·8 mm, width 6·3 mm; Fig. 173, BB 72307, length 3·8 mm, width 4·5 mm and Fig. 175, BB 72306, length 5·8 mm, width 7·0 mm; all from loc. 15, colln W8. Also recorded from locs 10–14, 16, 17, 21–3, 26 and 32, all in the Cheney Longville Formation.

DISCUSSION. See p. 248.

Dalmanella multiplicata (Bancroft) *prima* subsp. nov.
Figs 186–190

DESCRIPTION. Like *Dalmanella multiplicata* but with a brachial valve 75% as long as wide; divergent brachiophores with subparallel brachiophore bases 22% as long as the brachial valve and splaying laterally for 36% the length of the valve; dorsal muscle field 53% as long as the brachial valve; pedicle valve 86% as long as wide and 30% as deep as long; dental plates extend anteriorly for 21% of the length of the pedicle valve; ventral muscle field 28% as long as the pedicle valve and 34% as wide as the valve is long; radial ornamentation of costellae commonly 5 per mm, 2 mm anteromedially of the dorsal umbo.

DIMENSIONS.	length	width
Internal mould of pedicle valve, BB 72298, Fig. 190, holotype	3·6	4·3
Internal mould of pedicle valve, BB 72299, Fig. 189	3·5	4·2
Internal mould of brachial valve, BB 72300, Fig. 188	1·9	3·0
External and internal mould of brachial valve, BB 72301a b, Figs 186–7	3·1	4·8

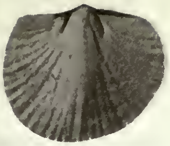
HORIZON AND LOCALITIES. Type material from loc. 3 (colln O60). Also recorded from locs 1, 2, 4–8, all in the Alternata Limestone Formation.

DISCUSSION. See p. 248.

Dalmanella unguis unguis (J. de C. Sowerby)
Figs 200–207

1839 *Terebratula unguis* J. de C. Sowerby *in* Murchison : 640; pl. 21, fig. 13.
1871 *Orthis unguis* (J. de C. Sowerby) Davidson : 257; pl. 37, figs 16–22.
1945 *Wattsella unguis* (J. de C. Sowerby) Bancroft : 196–197; pl. 23, figs 8–11; pl. 24, figs 6–7.
1958 *Dalmanella unguis* (J. de C. Sowerby) Dean : pl. 25, fig. 4.

Figs 181–218 *Dalmanella multiplicata multiplicata* (Bancroft), internal moulds of pedicle valves: 181 = BB 72313, ×2·5, 182 = BB 72312, ×2·3; internal and external moulds of brachial valves: 183 = BB 72310a, ×2·4, 184 = BB 72310b, ×2·2, 185 = BB 72311, ×2·5. *Dalmanella multiplicata prima* subsp. nov., internal and external moulds of brachial valves: 186 = BB 72301b, ×4·8, 187 = BB 72301a, ×3·8, 188 = BB 72300, ×4·3; internal moulds of pedicle valves: 189 = BB 72299, ×4·5, 190 = **holotype** BB 72298, ×4·8. *Dalmanella wattsi* (Bancroft), internal moulds of pedicle valves: 191 = BB 72316, ×1·5, 192 = BB 72315, ×1·5, 193 = BB 72314, ×1; internal and external moulds of brachial valves: 194 = BB 72317b, ×1·2, 195 = BB 72317a, ×1·2, 196 = BB 72318a, ×1·4, 197 = BB 72318b, ×1·1, 198 = BB 72336a, ×1·1, 199 = BB 72336b, ×1·3. *Dalmanella unguis unguis* (J. de C. Sowerby), internal and external moulds of brachial valves: 200 = BB 72322, ×2, 201 = BB 72321, ×2, 202 = BB 72323a, ×1·6, 203 = BB 72323b, ×1·4; internal moulds of pedicle valves: 204 = BB 72319, ×1·3, 205 = BB 72320, ×2·3, 206 = BB 72324, ×1·3, 207 = BB 72325, ×1·9. *Dalmanella unguis ultima* subsp. nov., internal moulds of pedicle valves: 208 = BB 72334, ×3·5, 209 = BB 72328, ×2·4, 210 = BB 72327, ×3, 217 = **holotype** BB 72326, ×4, 218 = BB 72335, ×2; internal and external moulds of brachial valves: 211 = BB 72332, ×5·2, 212 = BB 72331, ×3·2, 213 = BB 72329, ×2, 214 = BB 72330, ×2, 215 = BB 72333a, ×1·7, 216 = BB 72333b, ×1·7.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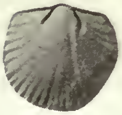
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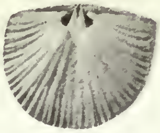
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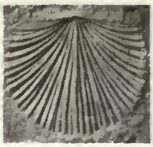
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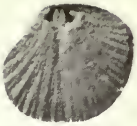
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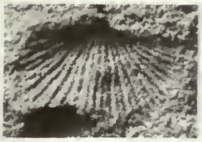
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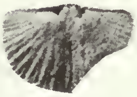
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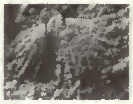
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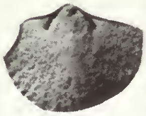
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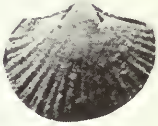
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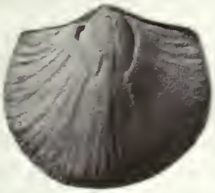
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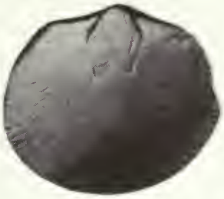
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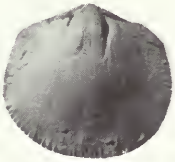
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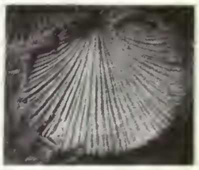
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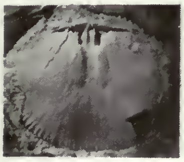
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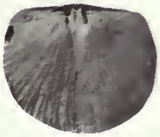
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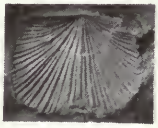
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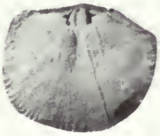
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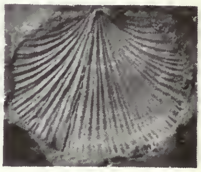
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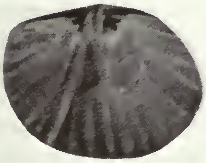
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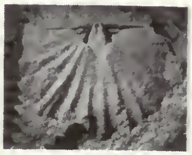
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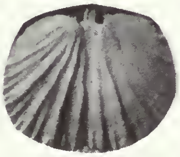
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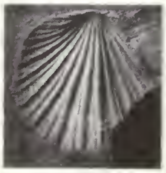
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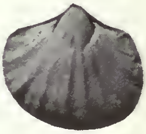
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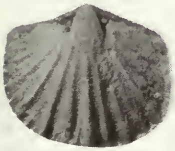
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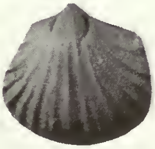
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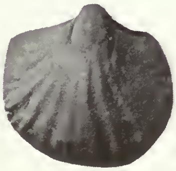
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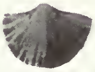
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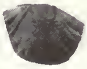
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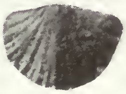
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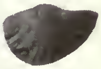
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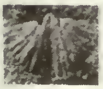
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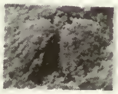
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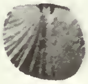
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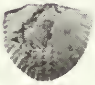
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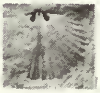
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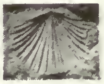
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Description. Large ventribiconvex *Dalmanella* with evenly convex brachial valve 81% as long as wide and with an obscure median sulcus; pedicle valve 87% as long as wide and 32% as deep as the valve is long; delthyrium and notothyrium open, pedicle callist obscure, ventral interarea moderately high, curved apscaline, longer than anacline dorsal interarea; radial ornamentation of very coarse plicae, commonly 2 or 3 ribs per mm, 2 mm anteromedially of the dorsal umbo; branching fairly simple with externals rarely developed.

Ventral muscle field bilobed with diductor muscles extending anteriorly for 39% of the length of the pedicle valve and appearing not to surround the median adductor muscle field; diductor muscle field 30% as wide as the pedicle valve is long; teeth small, stubby, with variably developed crural fossettes and supported by strong dental plates extending anteriorly for 22% the length of the pedicle valve and extending forward as strong convergent ridges bounding the diductor scars.

Dorsal interior with cardinal process consisting of a short, moderately thick linear shaft with expanded, rounded, crenulated single or bilobed myophore; brachiophores short, strong, divergent, with divergent bases flanking poorly-developed notothyrial platform and extending anteriorly for 20% of the length of the brachial valve and splaying laterally for 29% of the valve length; weakly impressed, elongately oval adductor scars poorly differentiated and separated posteriorly by a very low rounded median ridge and extending anteriorly for 49% of the length of the brachial valve; interior of valve often strongly ribbed and obscuring dorsal adductor scar.

Material and localities. Lectotype (selected Cocks 1978 : 63) GSM Geol. Soc. Colln 6864, from Cheney Longville Flags, 'Horderley' (exact locality unknown). Recorded here from the Crosspipes Member, loc. 27, colln M5 (e.g. Fig. 201, BB 72321, length 7·2 mm, width 8·8 mm; Fig. 204, BB 72319, length 13·2 mm, width 14·9 mm; Fig. 205, BB 72320, length 8·9 mm, width 9·4 mm) and loc. 24, colln WFT1 (e.g. Fig. 200, BB 72322; Figs 202–3, BB 72323; Figs 206–7, BB 72324–5). Also from locs 21, 29, 30 and 33.

Discussion. See p. 248.

Dalmanella unguis (J. de C. Sowerby) ***ultima*** subsp. nov.

Figs 208–218

Description. Like *Dalmanella unguis* but with a brachial valve 78% as long as wide; divergent brachiophores with slightly divergent brachiophore bases extending anteriorly for 33% of the length of the brachial valve and splaying laterally for 22% of length of valve; dorsal muscle field 54% as long as the brachial valve; pedicle valve 81% as long as wide and 26% as deep as long; dental plates extend anteriorly for 23% of the length of the pedicle valve; ventral muscle scar 35% as long as the pedicle valve and 40% as wide as the valve is long; radial ornamentation of costellae commonly 4 or 5 per mm, 2 mm anteromedially of the dorsal umbo.

Dimensions.	length	width
Internal mould of pedicle valve, BB 72326, holotype	3·1	3·9
Internal mould of pedicle valve, BB 72327	3·7	4·2
Internal mould of pedicle valve, BB 72328	3·5	5·0
Internal mould of brachial valve, BB 72329	5·8	6·6
Internal mould of brachial valve, BB 72330	5·8	6·5
Internal mould of brachial valve, BB 72331	3·0	3·7
Internal mould of brachial valve, BB 72332	1·7	2·2
External and internal moulds of brachial valve, BB 72333a, b	5·4	7·0
Internal mould of pedicle valve, BB 72334	2·8	3·6
Internal mould of pedicle valve, BB 72335	5·3	6·8

Horizon and localities. BB 72326–31 from loc. 47, colln CF1. BB 72332–5 from loc. 27, colln M8. Also recorded from loc. 21.

Discussion. See p. 248.

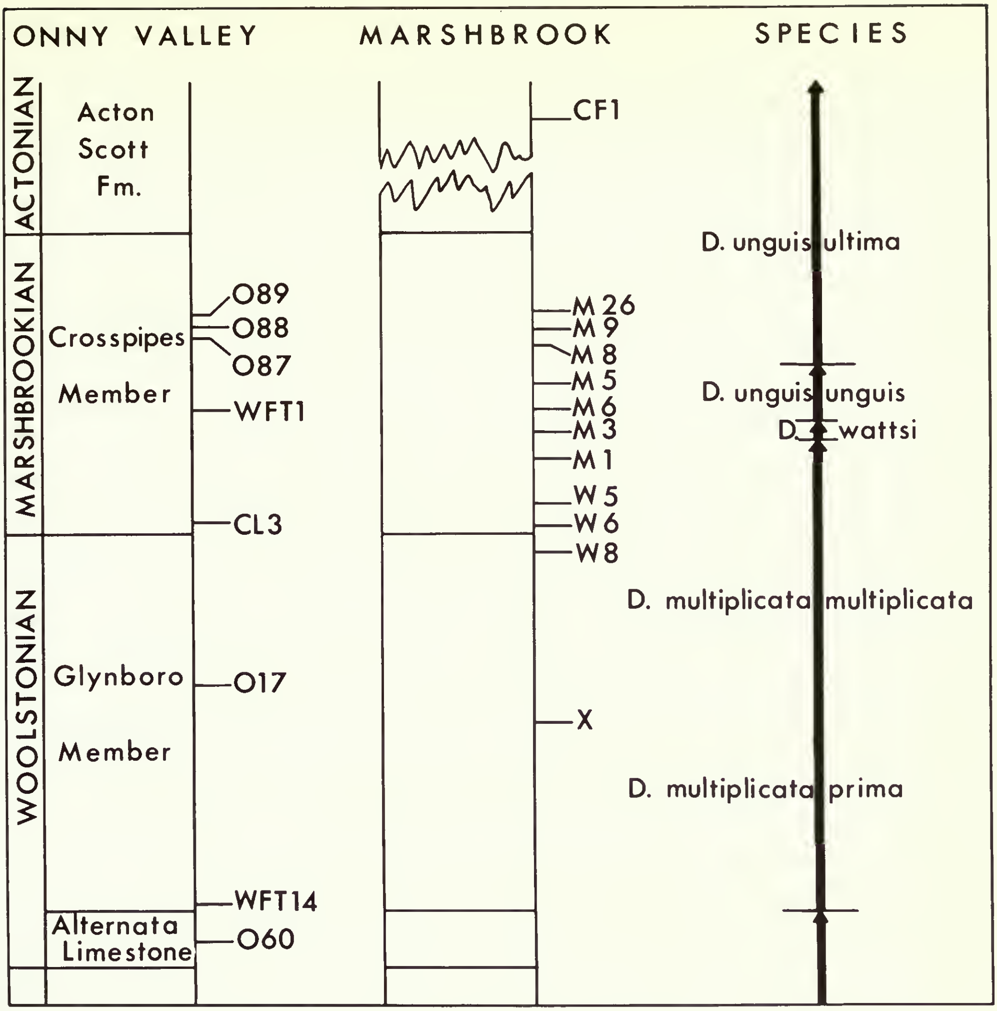
ONNY VALLEY
MARSHBROOK
SPECIES
ACTONIAN
Acton Scott Fm.
MARSHBROOKIAN
Crosspipes Member
WOOLSTONIAN
Glynboro Member
Alternata Limestone
O89
O88
O87
WFT1
CL3
O17
WFT14
O60
CF1
M 26
M 9
M 8
M 5
M 6
M 3
M 1
W 5
W 6
W 8
X
D. unguis ultima
D. unguis unguis
D. wattsi
D. multiplicata multiplicata
D. multiplicata prima

Fig. 219 The stratigraphical location of the *Dalmanella* samples used in the bivariate analysis in the Onny Valley and Marshbrook sections, and the range of the *Dalmanella* species and subspecies.

Dalmanella wattsi (Bancroft)

Figs 191–199

1928*a* *Wattsella wattsi* Bancroft : 58; pl. 1, figs 1–5.
1945 *Wattsella wattsi* Bancroft : 195–196; pl. 23, fig. 7; pl. 24, figs 2–5.
1958 *Dalmanella wattsi* (Bancroft) Dean : pl. 25, figs 2–3.
1963 *Dalmanella wattsi* (Bancroft); Williams & Wright : pl. 1, figs 2, 6, 9; pl. 2, fig. 3.

Description. Large ventribiconvex *Dalmanella* with an evenly, feebly convex brachial valve 82% as long as wide and with a shallow, often obscure median sulcus; pedicle valve 85% as long as wide and 23% as deep as the valve is long; delthyrium and notothyrium open, pedicle callist inconspicuous, ventral interarea moderately high, curved apscaline, longer than anacline dorsal interarea; radial ornamentation of coarse costellae, 3 or 4 per mm, 2 mm anteromedially of the dorsal umbo; branching complex, both externals and internals freely developed except on the first primary, which only has internals.

Ventral muscle field bilobed, with diductor muscles extending anteriorly for 38% of the length of the pedicle valve but not surrounding the median elongately oval adductor muscle field;

diductor muscle field 28% as wide as the pedicle valve is long; teeth small with variably developed shallow crural fossettes, and supported by strong dental plates extending anteriorly for 18% of the length of the pedicle valve and extending forward as strong, slightly convergent ridges bounding the diductor scars.

Dorsal interior with cardinal process consisting of strong, rounded shaft with expanded single or bilobed crenulated myophore extending slightly beyond the hinge; brachiophores very short, strongly divergent, with parallel bases flanking very well developed notothyrial platform and extending anteriorly for 18% of the length of the brachial valve, and splaying laterally for 30% of the valve length; weakly-impressed elongately oval adductor scars poorly differentiated, situated on either side of low, rounded median ridge and extending anteriorly for 45% of the length of the brachial valve.

MATERIAL AND LOCALITIES. Lectotype (selected Cocks 1978 : 63) BB 73833, from loc. 27, from which came colln M3, including Fig. 191, BB 72316, length 15·5 mm, width 19·4 mm; Fig. 192, BB 72315, length 17·0 mm, width 19·0 mm; Fig 193, BB 72314, length 16·8 mm, width 22·0 mm; Figs 194–5, BB 72317, length 14·0 mm, width 17·0 mm; Figs 196–7, BB 72318, length 13·2 mm, width 15·2 mm; Figs 198–9, BB 72336, length 14·5 mm, width 18·4 mm. Other specimens from loc. 31, also in the Crosspipes Member.

DISCUSSION. *Dalmanella* occurs sporadically throughout the Alternata Limestone Formation and Glynboro Member, but is particularly abundant in the uppermost part of the Glynboro Member and the Crosspipes Member. The calcareous sandstone Henley Member within the Acton Scott Formation at Acton Scott also yields a *Dalmanella.* Fig. 219 shows the stratigraphical positions, in two separate sections in the Caradoc district, of the samples used to derive the statistics given in Tables 43–53. The overwhelming abundance of *Dalmanella* populations precludes a bed-by-bed bivariate analysis. The sampling interval chosen for statistical analysis of the populations was primarily dictated by outcrop availability, but where sedimentary facies changes occurred, a close sampling interval was employed. A qualitative assessment of *Dalmanella* populations was made between each measured collection.

Only one measurable population of *Dalmanella multiplicata prima* subsp. nov. (colln O60, loc. 63) was available from the Alternata Limestone, and this differed significantly from the stratigraphically younger colln WFT14 (loc. 14), in having a brachial valve which increased in width faster ($P < 0{\cdot}01$) and in its longer ventral muscle scar ($P < 0{\cdot}05$). Further, the O60 population differs significantly from the topotype *D. multiplicata multiplicata* (Bancroft) population (colln x; loc. 18), in having a brachial valve which increased in width faster ($P < 0{\cdot}01$) and in faster growth in relative depth of the pedicle valve ($P < 0{\cdot}02$). In other respects, including ribbing (Table 53), the new subspecies closely resembles *D. multiplicata multiplicata.* In view of these morphological differences only a new subspecies has been recognized, so as to emphasize the close relationship with *D. multiplicata multiplicata.* The new subspecies appears to be limited to the Alternata Limestone.

The upper Glynboro Member and the lower part of the Crosspipes Member (up to and including the *Dalmanella wattsi* Zone of Bancroft 1929*a*, *b*,1933) contain abundant *Dalmanella* populations with much morphological variation. The *D. multiplicata multiplicata* topotype population (colln x) differs significantly from the W8 population in having relatively narrower dorsal cardinalia ($P < 0{\cdot}05$) and faster increase in relative length of the ventral muscle field. The W8 population does not differ from the W6 population with respect to any character, and in turn the W6 population does not differ from the W5 population nor from the M1 population (see Fig. 219).

Dalmanella population CL3 does not differ in any character from population W5, and only differs from the older population O17 in having relatively wider dorsal cardinalia ($P < 0{\cdot}05$). The O17 population does not differ in any character from the WFT14 population, which in turn differs solely from the topotype population of *D. multiplicata multiplicata* in having relatively wider dorsal cardinalia ($P < 0{\cdot}05$).

In view of the non-directional but persistent morphological variation expressed by *Dalmanella* populations in the Glynboro and lower Crosspipes Members (to the top of the *D. wattsi* Zone of Bancroft 1929*a*, *b*, 1933), in both sections, it is proposed to include all the populations present in the one subspecies, *D. multiplicata multiplicata* (Bancroft). This is supported by the limited data on ribbing (Table 53), which show that there is no significant difference in ribbing densities of the *D. multiplicata* topotype population and the younger population (M1) of the same species.

Bancroft (1928*a*, 1945) gave the type locality for *Dalmanella wattsi*, in the old quarry in Marshwood (loc. 27), in the *Heterorthina praeculta* beds, 3 in (76 mm) below the base of the '*Wattsella*' *unguis* beds. The topotype population (collection M3) differs significantly from the stratigraphically older M1 population on four counts, the relatively wider brachial valve ($P < 0{\cdot}05$), the slower increase in length of the dorsal cardinalia ($P < 0{\cdot}05$), the relatively longer pedicle valve ($P < 0{\cdot}05$) and the slower increase in ventral muscle field width ($P < 0{\cdot}01$). The fact that the brachial valve is significantly wider and the pedicle valve significantly longer probably reflects that the pedicle interarea of *D. wattsi* is longer than that of the M1 population and as such the increase in posterior growth of the interarea is greater relative to the increase in valve width. Further, in *D. wattsi* the ribbing is significantly coarser ($P < 0{\cdot}001$) than the M1 population of *D. multiplicata multiplicata*.

The topotype population of *D. wattsi* does not differ from the topotype *D. multiplicata multiplicata* in bivariate characters, but their ribbing is different. In *D. wattsi* the ribbing is significantly coarser ($P < 0{\cdot}001$). Bancroft (1928*a*) maintained that *D. wattsi* could be differentiated on a series of costellae insertions (Table 11). However, the only significant difference is the earlier insertion of 4å relative to 4b in *D. wattsi*. *D. wattsi* has only been found in the Marshbrook area (locs 27 and 31).

The topotype population (colln M6; loc. 27) of *D. unguis* differs from *D. wattsi* in the faster increase in length of the dorsal cardinalia ($P < 0{\cdot}01$), the relatively wider pedicle valve ($P < 0{\cdot}05$), the slower growth in relative depth of the pedicle valve ($P < 0{\cdot}05$) and the wider ventral muscle scar ($P < 0{\cdot}05$). *D. unguis* (colls M5 and M6 pooled) has significantly coarser ribbing ($P < 0{\cdot}05$). From the topotype population of *D. multiplicata multiplicata*, *D. unguis* differs in having significantly coarser ribbing ($P < 0{\cdot}001$), faster increase in length of the dorsal cardinalia ($P < 0{\cdot}02$) and slower growth in relative depth of the pedicle valve ($P < 0{\cdot}001$).

The *Dalmanella* populations present in the upper part (*D. unguis* and *O. reuschi* Zones of Bancroft 1929*a*, *b*) of the Crosspipes Member also display a great deal of morphological variability. Population M5, which occurs stratigraphically above the topotype *D. unguis* population, differs in having relatively longer dorsal cardinalia ($P < 0{\cdot}01$) and faster growth in relative depth of the pedicle valve. There is no ribbing difference.

There is no significant bivariate character difference between *Dalmanella* populations M5–M8, M8–M9 and M9–M26. Population WFTI differs from the topotype of *D. unguis* in having relatively shorter dorsal cardinalia ($P < 0{\cdot}01$) and in the faster increase in length of the dorsal adductor muscle field. Further, the WFTI population does not differ, as regards bivariate characters, from the stratigraphically younger O87–89 population. However, this latter population differs from the youngest population in the Marshbrook section (M26) in the faster increase in relative width of the brachial valve ($P < 0{\cdot}01$).

Thus the *Dalmanella* populations of the Upper Cheney Longville Formation show no consistent morphological variation. However, the populations in the upper part of the *D. unguis* Zone, in both sections, show a consistent difference from the older populations, in having finer ribs (Table 53). The M6, M5 and WFTI populations do not differ significantly as regards coarseness of ribbing. However, the younger populations of M8–M9 (pooled data) differ from M6, M5 and WFTI (all at $P < 0{\cdot}001$), whilst O87–89 differs from the same collections ($P < 0{\cdot}01$). This consistent morphological difference is afforded taxonomic recognition, with the erection of the subspecies *D. unguis ultima* to cover forms with a modal rib count of 4 or 5 per mm, at 2 mm anteromedially from the dorsal umbo, as opposed to the 2 or 3 of *D. unguis unguis*.

In calcareous bioturbated sandstones of the stratigraphically younger Acton Scott Formation *D. unguis ultima* briefly reappears (loc. 47). The population CF1 does not differ from the previous populations of the subspecies, in either bivariate statistics or ribbing.

Dean (1958 : 205) reported sympatry between *D. wattsi* and *D. unguis*, at least in the Marshbrook area. This is contrary to the findings here. Large collections of basal *D. unguis* Zone specimens show a wide range of continuous morphological variation especially with respect to ribbing, which is the easiest qualitative character by which to distinguish the two species. Presumably Dean would place the finer-ribbed specimens in *D. wattsi*, but this would involve splitting a continuous morphological series into two categories and would be unjustified.

Genus *BANCROFTINA* Sinclair, 1946

1933 *Raymondella* Bancroft : 3 (*nomen nudum*).
1938 *Raymondella* Bancroft; Whittington : 249 (*non* Reed 1935 : 8).
1945 *Raymondella* Bancroft : 197.
1946 *Bancroftina* Sinclair : 295.

DIAGNOSIS (emended). Subcircular to subquadrate ventribiconvex shells with shallow sulcate brachial valve; radial ornamentation finely costellate with first order costellae branching internally, more commonly than externally, in the first four sectors. Ventral interarea moderately long, curved and apscaline with open delthyrium; dorsal interarea short, weekly curved, anacline, notothyrium open and commonly filled with cardinal process; shell punctate.

Ventral interior with massive teeth supported by well-developed subparallel to divergent dental lamellae; muscle field subtriangular to bilobed in outline with submedian diductor lobes not enclosing median adductor scar; pedicle callist well developed; pallial sinus pattern unknown.

Dorsal interior with stout bilobed or trilobed cardinal process; brachiophores very stout and short, widely divergent with their bases greatly divergent relative to their tops and often subparallel to hinge line; fulcral plates rarely developed; ancillary struts often strong, fused to well-developed median ridge; dorsal adductor scar elongately oval and bipartite or quadripartite.

TYPE SPECIES. *Raymondella typa* Whittington, by original definition of Sinclair (1946 : 295).

DISCUSSION. Bancroft (1933 : 3) initially proposed the name *Raymondella*, with *R. typa* as genotype, for a group of middle Caradoc dalmanellid brachiopods from the upper Horderley Sandstone, Alternata Limestone and lower Longville Flags (all Longvillian) of the type Caradoc. The diagnosis was inadequate and most subsequent workers (see Williams & Wright 1963 : 27) have treated this as a *nomen nudum*. However, Whittington (1938 : 249) fully described *Raymondella typa*, based on composite material including specimens of his own from silty ashes of the Berwyn Dome and the material Bancroft had at his disposal. Whittington attributed the genus and the species to Bancroft. *Raymondella* was further described by Bancroft (1945) but as the authorship of the genus has to be attributed to the first full description of Whittington (1938), the name was by that time occupied (Reed 1935). Thus Sinclair (1946, 1949) proposed the name *Bancroftina* to cover the Caradoc dalmanellid and designated *Raymondella typa* Whittington as the type species.

Bancroftina hewitti sp. nov.
Figs 247–250

DESCRIPTION. Large subcircular, unequally biconvex *Bancroftina*, with shallow sulcate brachial valve 79% as long as wide and less than one-tenth as deep as long, and pedicle valve 80% as long as wide and 28% as deep as long; radial ornamentation moderately coarsely costellate with a modal count of 4 costellae per mm, 2 mm anterior of the dorsal umbo, external branching earlier

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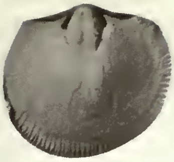
Figs 220–246 *Bancroftina whittingtoni* sp. nov., internal moulds of pedicle valves: 220 = BU 241, ×1·8, 221 = BB 73681, ×2, 222 = BB 72469, ×1·5, 223 = BB 73677, ×1·7, 224 = BB 73678, ×1·9, 225 = BB 72467, ×2, 226 = BB 72468, ×1·8; internal and external moulds of brachial valves: 227 = **holotype** BB 72475, ×1·8, 228 = BB 72476, ×1·9, 229 = BB 72472, ×1·9, 230 = BB 72473, ×1·9, 231 = BB 72471, ×1·7, 232 = BB 72474, ×1·7, 233 = BB 72470, ×1·9. *Bancroftina typa* (Whittington), internal moulds of pedicle valves: 234 = BB 72480, ×2, 235 = BB 72481, ×2, 244 = BB 72479, ×1·3, 245 = BB 72486, ×1·1, 246 = BB 72487, ×1·6; internal and external moulds of brachial valves: 236 = BB 72483, ×2, 237 = BB 72482, ×2, 238 = lectotype BU 242, ×1·8, 239 = lectotype of *robusta* BB 10302, ×2·5, 240 = BB 72484, ×1·8, 241 = BB 72477, ×1·9, 242 = BB 72478, ×1·5, 243 = BB 72485, ×1·7.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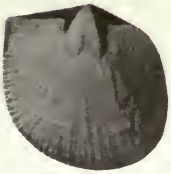
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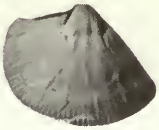
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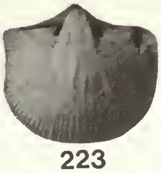
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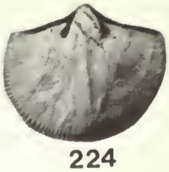
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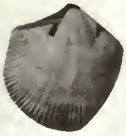
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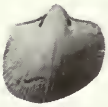
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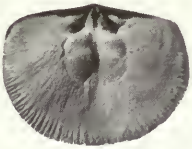
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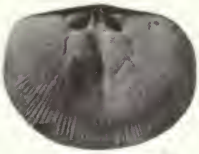
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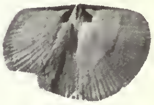
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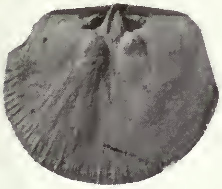
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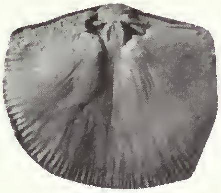
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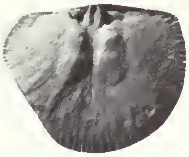
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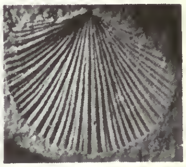
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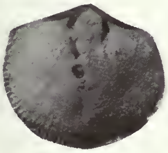
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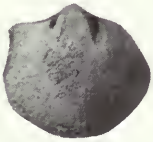
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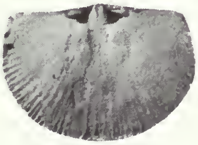
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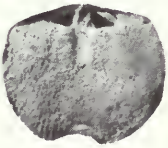
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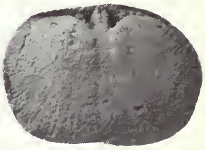
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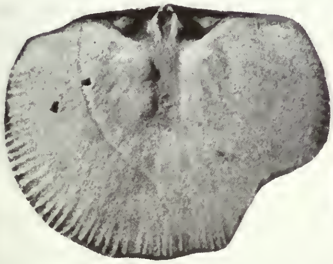
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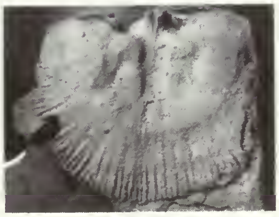
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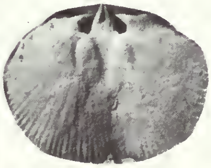
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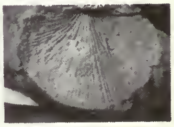
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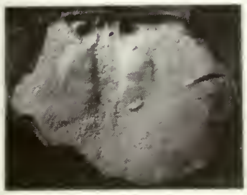
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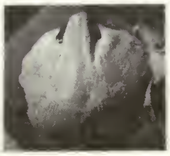
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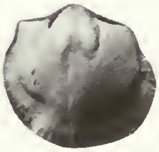
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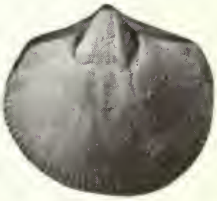
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than internal slightly more common in sectors I to IV; dental lamellae very strong, weakly divergent and extending anteriorly for 17% of the length of the valve, crural fossettes absent, ventral muscle scar extending anteriorly for 35% of the length of the valve and 30% as wide as the valve is long; heavily calcified cardinalia with divergent brachiophore bases 14% the length of the brachial valve and 27% as wide as the valve is long; ancillary struts massive, ankylosed to median ridge, bipartite dorsal adductor scar extending anteriorly for 42% the length of the valve.

NAME. After Dr R. A. Hewitt.

DIMENSIONS.	length	width
Internal mould of brachial valve, BB 72488, holotype	19·3	23·0
Internal mould of pedicle valve, BB 72489	16·7	18·6
Internal mould of brachial valve, BB 72490	16·7	20·1
Internal mould of pedicle valve, BB 72491	18·3	23·6

HORIZON AND LOCALITIES. All figured specimens from loc. 32; holotype BB 72488, colln LM4, remainder colln LM6. Also recorded from locs 26 and 27.

DISCUSSION. See p. 253.

Bancroftina typa (Whittington)
Figs 234–246

1933 *Raymondella typa* Bancroft : 3; *nomen nudum.*
1938 *Raymondella typa* Bancroft; Whittington : 249 *pars*; pl. 10, fig. 13, *non* figs 12, 14.
1945 *Raymondella typa* Bancroft; Bancroft : 198–201; pl. 25, figs 1–10.
1945 *Raymondella robusta* Bancroft : 201; pl. 25, figs 11, 12; pl. 26, figs 1–3.
1946 *Bancroftina typa* (Bancroft) Sinclair : 295.
1959 *Bancroftina typa* (Whittington); Cave & Dean : 294; pl. 53, figs 5, 6.
1963 *Bancroftina typa* (Whittington); Williams & Wright : 7; pl. 1, figs 12, 15; pl. 2, fig. 6.
1963 *Bancroftina robusta* (Bancroft) Williams & Wright : pl. 1, fig. 13.

DESCRIPTION. Subcircular to subquadrate, unequally biconvex *Bancroftina*, with shallow sulcate brachial valve 79% as long as wide and less than one-eighth as deep as long, and pedicle valve 87% as long as wide and 30% as deep as long; radial ornamentation finely costellate with a modal count of 5 costellae per mm, 2 mm anterior of dorsal umbo, external branching very rarely occurring earlier than internal in sectors I to IV; dental lamellae strongly developed, divergent and extending anteriorly for 21% of the length of the valve, with moderately strong crural fossettes; ventral muscle scar extending anteriorly for 35% of the length of the valve and 32% as wide as the valve is long; strong cardinalia with widely divergent brachiophore bases 19% the length of the brachial valve and 34% as wide as the valve is long; bipartite dorsal adductor scar extending anteriorly for 50% the length of the valve.

MATERIAL AND LOCALITIES. Lectotype (Fig. 238) BU 242 (selected Cave & Dean 1959 : 295), length 10·7 mm, width 14·7 mm, from small quarry in upper Horderley Sandstone at New House, grid ref. SO 418859, from which also came BB 72480 (Fig. 234), length 10·1 mm, width 11·7 mm; BB 72481 (Fig. 235), length 9·7 mm, width 10·4 mm; BB 72482 (Fig. 237), length 9·5 mm, width 10·6 mm; BB 72483 (Fig. 236), length 9·5 mm, width 13·2 mm. From loc. 14, colln WFT19, e.g. BB 72477 (Fig. 241), length 12·4 mm, width 15·2 mm; BB 72478 (Fig. 242), length 9·7 mm, width 13·0 mm; BB 72479 (Fig. 244), length 13·8 mm, width 16·4 mm. From loc. 19, e.g. BB 10302 (Fig. 239), lectotype of *robusta*, length 13·6 mm, width 17·6 mm. From loc. 17, colln S9, e.g. BB 72484–7 (Figs 240, 243, 245–6). Also from locs 1–8, 10 and 16.

Bancroftina whittingtoni sp. nov.
Figs 220–233

1938 *Raymondella typa* Bancroft; Whittington : 249 *pars*; pl. 10, figs 12, 14, *non* fig. 13.

DESCRIPTION. Semicircular to subquadrate, unequally biconvex *Bancroftina*, with shallow sulcate brachial valve 77% as long as wide and less than one-eighth as deep as long, and pedicle valve 81% as long as wide and 34% as deep as long; radial ornamentation very finely costellate with modal count of 7 costellae per mm, 2 mm anterior of dorsal umbo; in sectors I to IV internal branching occurs earlier than external branching; dental lamellae strongly developed, subparallel to slightly divergent, and extending anteriorly for 20% of the length of the valve, ventral muscle scar extending anteriorly for 32% of the length of the valve and 31% as wide as the valve is long; strong cardinalia with widely divergent brachiophore bases extending anteriorly for 20% the length of the brachial valve and 32% as wide as the valve is long; dorsal adductor scar extending anteriorly for 53% the length of the valve.

NAME. After Professor H. B. Whittington.

DIMENSIONS.	length	width
Internal mould of brachial valve, BB 72475, holotype	12·3	13·8
Internal mould of pedicle valve, BB 73678	10·5	13·2
Internal mould of pedicle valve, BU 241	13·2	15·2
Internal mould of pedicle valve, BB 73677	10·8	12·5
Internal mould of pedicle valve, BB 72467	9·5	10·6
Internal mould of pedicle valve, BB 72468	7·5	8·0
Internal mould of pedicle valve, BB 72469	12·6	16·0
External mould of brachial valve, BB 72470	9·9	12·2
Internal mould of brachial valve, BB 72471	14·3	17·2
Internal mould of brachial valve, BB 72472	7·5	10·7
Internal mould of brachial valve, BB 72473	12·9	15·2
Internal mould of brachial valve, BB 72474	12·7	14·8

HORIZON AND LOCALITIES. This species is known only from the type beds in the Berwyn Hills (Whittington 1938). The sample used in this study comes from a disused quarry in the Bryngwyn Beds, 360 m north-east of the spot height in the ancient camp at Bryngwyn Hill, some 4·8 km south-west of Llansantffraid; SJ 188184.

DISCUSSION. *Bancroftina* is very abundant in the upper Horderley Sandstone, Alternata Limestone and lower Cheney Longville Formation. Bancroft (1945) recognized *Bancroftina typa* (Whittington) from the Horderley Sandstone and erected a new species *B. robusta*, from the lower Cheney Longville Formation. Previously, Bancroft (1933 : table adjacent to p. 4) had referred to an undescribed species of *Bancroftina*, *B. gigantea* (a *nomen nudum*), as characterizing 165 ft (50 m) of strata, in east Shropshire (Salop), above his *Kjaerina bipartita* Zone (= Alternata Limestone). The type locality of *B. robusta* falls within his zone of *B. gigantea*, suggesting that he was in fact referring to the same species.

The statistical data derived in Tables 54–64 are based on collections which Whittington described as *B. typa* from the Berwyn Hills, *B. typa* from the Horderley Sandstone and *B. robusta*. As Bancroft (1945 : 201) emphasized the importance of size in the species classification of this genus, populations with the largest and smallest individuals and a population from the Alternata Limestone and upper Cheney Longville Formation have also been statistically analysed.

As regards bivariate statistics, *Bancroftina* from the Horderley Sandstone, Alternata Limestone and Glynboro Member, including *B. typa* and *B. robusta* topotypes, do not differ significantly. *Bancroftina* from the Berwyn Hills, north Powys, differs consistently from the above populations in having a slower relative increase in width of the dorsal cardinalia ($P<0{\cdot}05$–$0{\cdot}001$) and relatively longer dorsal cardinalia ($P<0{\cdot}05$–$0{\cdot}01$) and so a new species, *B. whittingtoni*, is described here. *B. hewitti* does not differ significantly from the older populations of *Bancroftina* from Salop but does differ significantly from the Berwyn Hills *Bancroftina* in having relatively shorter dental lamellae ($P<0{\cdot}05$).

B. whittingtoni from the Berwyn Hills has significantly finer ribbing (see Table 64) than *B. hewitti* ($P<0{\cdot}001$) and the remaining *Bancroftina* populations ($P<0{\cdot}01$). *B. hewitti* differs significantly ($P<0{\cdot}01$) from the other Salop populations in having the coarsest costellae.

The earlier insertion of eight costellae relative to eight others has been analysed (see Table 63). 1b̄)1å, 2b̄)2å, 3āl̄ā)2å, 3āl̄̇)3b̄l̄ and 4b̄)4b̊ are constantly associated throughout the seven populations of the three species. 2āl̄)2b̄ is very variable, forming no consistent patterns. *B. hewitti* differs significantly from the other species in the earlier insertion of 3å relative to 3āl̄ā ($P < 0{\cdot}001$) and 3å relative to 3c̄ ($P < 0{\cdot}001$). These two rib patterns are constantly associated in *B. typa* and *B. whittingtoni.*

To summarize, there are three species of *Bancroftina* in the Caradoc of Wales and the Welsh Borderland:

1. *B. whittingtoni* from the Berwyn Hills, which differs from *B. typa* in the configuration of the dorsal cardinalia and in having finer ribbing. From *B. hewitti* it differs in its finer ribbing and dental lamellae.
2. *B. typa*, which includes populations from the Horderley Sandstone originally assigned by Bancroft to *B. robusta.*
3. *B. hewitti*, which is characterized by its coarse ribbing and the costellae insertions 3c̄)3å and 3āl̄ā)3å. Further, the species has very heavily calcified dorsal cardinalia with secondary calcite deposition around the brachiophores forming large blocks. Its ancillary struts are very strong and in the pedicle valve it does not possess crural fossettes as do *B. whittingtoni* and *B. typa.*

Genus ***CRYPTOTHYRIS*** Bancroft, 1945

DIAGNOSIS (emended). Subcircular, unequally biconvex dalmanellid with a deeply convex pedicle valve and sulcate brachial valve; radial ornamentation multicostellate; ventral interarea moderately long, curved, apscaline with open delthyrium and prominent umbo; dorsal interarea short and curved, anacline, notothyrium filled by cardinal process; shell punctate.

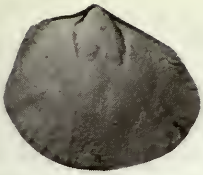
Ventral interior with massive teeth supported by strong subparallel dental plates with strong crural fossettes on their medial faces, pedicle callist well developed, muscle field subtriangular to cordate in outline, submedian diductor lobes extending beyond dental lamellae and not surrounding anterior edge of median adductor field.

Dorsal interior with stout, undifferentiated, bilobed and anteriorly crenulated cardinal process, brachiophores with massive triangular pads and with their bases slightly divergent relative to their tops, fulcral plates rarely developed; dorsal adductor scar elongate and impressed, quadripartite about strong median ridge.

DISCUSSION. Bancroft (1928*a*, 1945) and more recently Kemežys (1968) noted that *Cryptothyris* had rhipidomelloid ribbing. However, in internal features this genus belongs unequivocally in the Dalmanellidae, an assignment made in 1965 by Williams *et al.*

TYPE SPECIES. *Resserella paracyclica* Bancroft, 1928.

Figs 247–275 *Bancroftina hewitti* sp. nov., internal moulds of pedicle valves: 247 = BB 72491, ×1·2, 248 = BB 72489, ×1·2; internal moulds of brachial valves: 249 = **holotype** BB 72488, ×1·4, 250 = BB 72490, ×1·2. *Cryptothyris paracyclica* (Bancroft), internal moulds of brachial valves: 251 = lectotype BB 24172, ×2·5, 252 = BB 72502, ×1·9, 253 = BB 73564, ×2·4, 254 = BB 24184, ×1·7, 255 = BB 24180, ×1·6, 256 = BB 72499, ×2·2, 257 = BB 72498, ×2; external surface of brachial valve: 258 = BB 72500, ×2·5; internal moulds of pedicle valves: 260 = BB 24220, ×2, 261 = BB 24221, ×2, 262 = BB 72501, ×1·5, 263 = BB 24216, ×2, 264 = BB 24222, ×1·1, 265 = BB 72496, ×1·6, 266 = BB 72497, ×1·6; external surface of pedicle valve and lectotype of synonymized *C. cyclica*: 259 = BB 24218, ×2·5. *Onniella avelinei* Bancroft, internal mould of brachial valve: 267 = lectotype, BB 10326, ×2. *Onniella reuschi* Bancroft, internal and external moulds of brachial valves: 268 = BB 72414, ×1·7, 269 = BB 72415, ×1·8, 270 = BB 72412, ×1·5, 271 = BB 72413, ×1·4, 272 = BB 72422, ×2, 273 = BB 72420, ×2·5, 274 = BB 10248 (lectotype of synonymized *O. aspasia*), ×3, 275 = BB 72423, ×1·9.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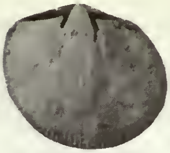
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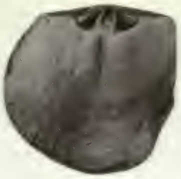
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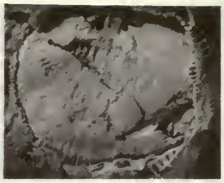
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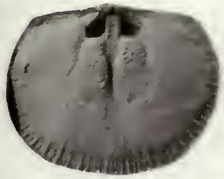
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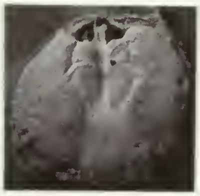
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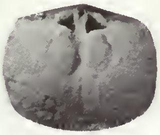
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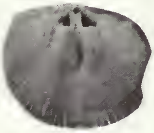
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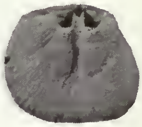
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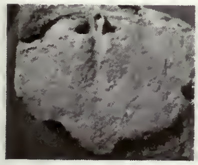
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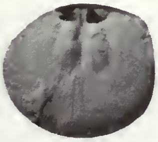
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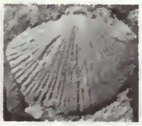
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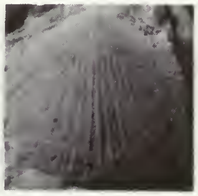
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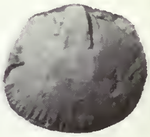
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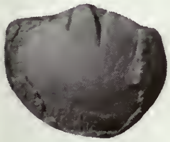
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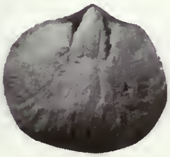
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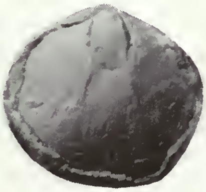
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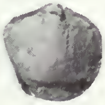
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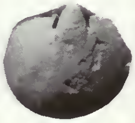
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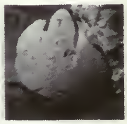
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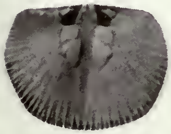
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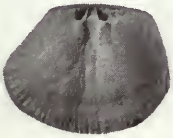
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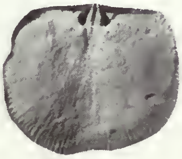
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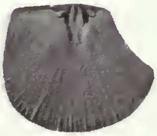
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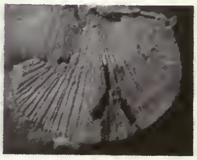
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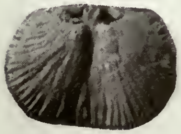
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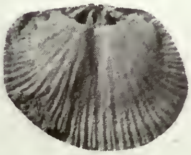
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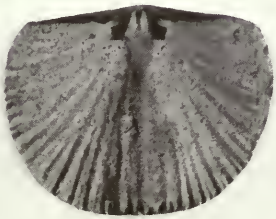
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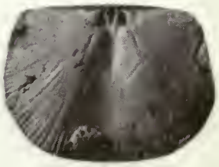
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Cryptothyris paracyclica (Bancroft)

Figs 251–266

1928*a* *Resserella paracyclica* Bancroft : 56; pl. 1, figs 6–9.
1928*a* *Resserella cyclica* Bancroft : 56; pl. 1, fig. 10.
1945 *Cryptothyris paracyclica* (Bancroft) Bancroft : 223.
1958 *Cryptothyris paracyclica* (Bancroft); Dean : pl. 25, fig. 7.
1963 *Cryptothyris paracyclica* (Bancroft); Williams & Wright : pl. 2, figs 9, 14, 15.

DESCRIPTION (emended). Subcircular, unequally biconvex *Cryptothyris*, with evenly convex brachial valve 80% as long as wide, and pedicle valve 82% as long as wide and 30% as deep as long; radial ornamentation finely costellate with modal count of 4 costellae per mm, 2 mm anteromedially of the dorsal umbo, median costellae commonly developed; subparallel dental lamellae 20% as long as pedicle valve, ventral muscle scar extending anteriorly for 36% the length of the valve and 32% as wide as the valve is long; cardinalia massive with very slightly divergent brachiophore bases extending anteriorly for 19% the length of the valve and splaying laterally for 31% of the valve length; dorsal adductor scar extending anteriorly for 54% of the length of the valve.

MATERIAL AND LOCALITIES. Lectotype (Fig. 251) BB 24172 (selected Cocks 1978 : 64), length 9·2 mm, width 11·3 mm; lectotype of *cyclica* (Fig. 259) BB 24218, length 9·2 mm, width 9·6 mm; also Fig. 253, BB 73564, length 7·1 mm, width 9·4 mm; Fig. 254, BB 24184, length 10·0 mm, width 11·7 mm; Fig. 255, BB 24180, length 9·7 mm, width 11·2 mm; Fig. 257, BB 72498, length 11·1 mm, width 13·0 mm; Fig. 258, BB 72500, length 5·6 mm, width 6·9 mm; Fig. 260, BB 24220, length 8·5 mm, width 9·6 mm; Fig. 261, BB 24221, length 8·9 mm, width 11·0 mm; Fig. 263, BB 24216, length 12·0 mm, width 14·3 mm; Fig. 264, BB 24222, length 10·9 mm, width 12·0 mm; all from loc. 39. Also loc. 44, colln OA1 (e.g. Figs 256, 265–6, BB 72499, BB 72496–7), loc. 43, colln CP2 (e.g. Fig. 252, BB 72502, and Fig. 262, BB 72501). Also recorded from locs 40–2, 45 and 48, all from the Acton Scott Formation.

DISCUSSION. Bancroft (1928*a*, 1945) erected *Resserella paracyclica* and *R. cyclica*, which he later transferred to *Cryptothyris*, from the same type locality in the Acton Scott Formation of the Onny Valley, and distinguished between them by the width of the hinge line. At the type locality *Cryptothyris* is very rare, but from a study of the small amount of Bancroft material in the BM(NH) it is apparent that, as regards hinge width, there is continuous variation between the two species and thus *C. cyclica* is treated as being synonymous with *C. paracyclica*. At loc. 44 in the Acton Scott Formation of Marshbrook a small collection of *C. paracyclica* has been statistically analysed to give some idea of the variation of the species involved (see Tables 65–73).

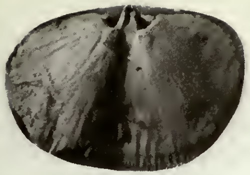
Genus *ONNIELLA* Bancroft, 1928

Onniella broeggeri Bancroft

Figs 316–335

1928*a* *Onniella bröggeri* Bancroft : 56–57; pl. 2, figs 1–5.
1945 *Onniella bröggeri* Bancroft; Bancroft : 222–223; pl. 30, figs 16–17.

Figs 276–305 *Onniella reuschi* Bancroft, internal moulds of brachial valves: 276 = BB 72425, ×2, 277 = BB 72424, ×2·4, 278 = BB 72431, ×1·5, 279 = BB 72432, ×1·7; internal moulds of pedicle valves: 280 = BB 72417, ×1·8, 281 = BB 10239 (lectotype of synonymized *O. grandis*), ×2, 282 = BB 72411, ×2·4, 283 = BB 72408, ×1·7, 284 = BB 72410, ×1·8, 285 = BB 72418, ×2, 286 = BB 72421, ×2, 287 = BB 72419, ×2·2, 288 = BB 72428, ×1·7, 289 = BB 72427, ×2·5, 290 = BB 72426, ×3, 291 = BB 72430, ×1·7, 292 = BB 72429, ×2·9, 293 = BB 72409, ×1·7. *Onniella depressa* Bancroft, conjoined valves: 294 = brachial view of BB 10254 (lectotype of synonymized *O. sinuata*), ×1·5, 295 = pedicle view of BB 10254, ×1·5, 296 = brachial view of lectotype BB 10251, ×1·5, 297 = pedicle view of lectotype BB 10251, ×1·5; internal moulds of pedicle valves, 298 = BB 72435, ×4, 299 = BB 72466, ×4, 300 = BB 72434, ×2·5, 301 = BB 72444, ×2·5, 302 = BB 72433, ×2·5, 303 = BB 73679, ×2·5, 304 = BB 72443, ×2·5, 305 = BB 72441, ×2·5.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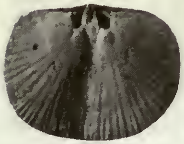
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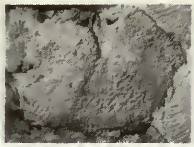
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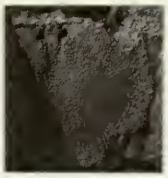
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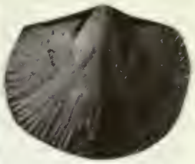
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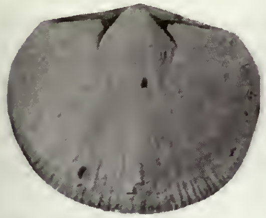
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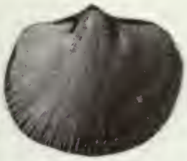
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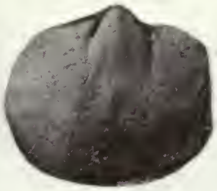
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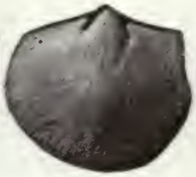
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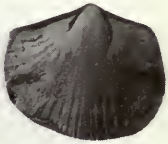
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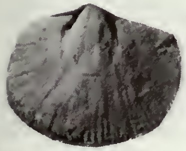
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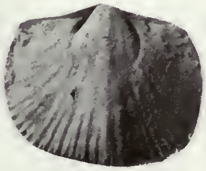
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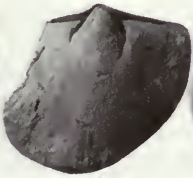
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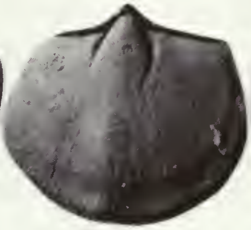
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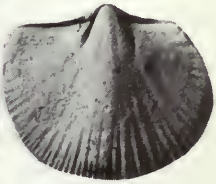
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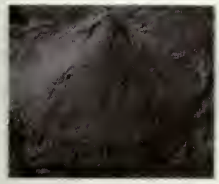
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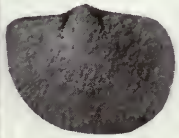
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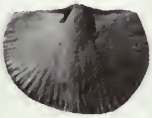
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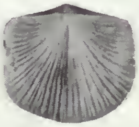
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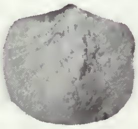
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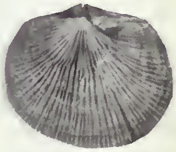
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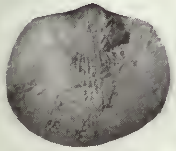
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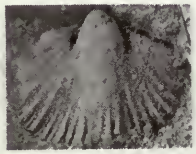
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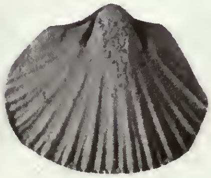
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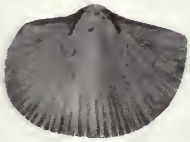
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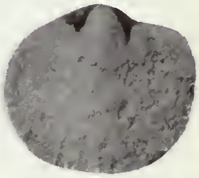
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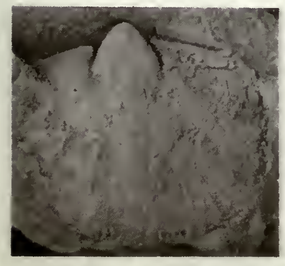
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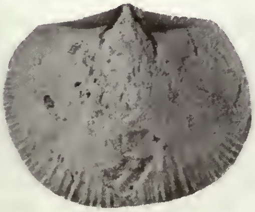
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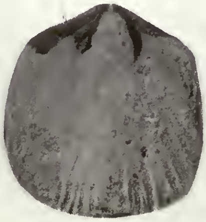
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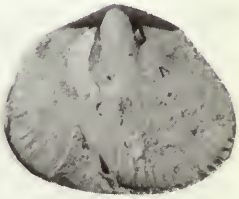
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1945 *Onniella inconstans* Bancroft : 221–222; pl. 31, figs 1–3.
1958 *Onniella inconstans* Bancroft; Dean : pl. 25, figs 8–9.
1958 *Onniella broeggeri* Bancroft; Dean : pl. 25, figs 10–11.
1965 *Onniella broeggeri* Bancroft; Cave : pl. 12, figs F, I, L, O, P.

DESCRIPTION (emended). Subquadrate, unequally biconvex *Onniella*, with evenly convex, sulcate brachial valve 76% as long as wide, and pedicle valve 82% as long as wide and 28% as deep as long; shell with right-angular cardinal extremities; dorsal interarea short, curved, anacline, notothyrium open; ventral interarea moderately long, curved apscaline, delthyrium open; radial ornamentation commonly 6 costellae per mm, 2 mm anterior of dorsal umbo, branching freely developed.

Ventral interior with massive stout teeth supported by subparallel to parallel dental lamellae, which extend anteriorly for 22% of the length of the valve, and have moderately strong to very strong crural fossettes on their inner faces; dental plates continued along sides of diductor muscle field as a pair of strong ridges; adult ventral muscle field angular subpentagonal and extending anteriorly for 34% of length of the pedicle valve, maximum width 30% of the valve length; diductor scars elongately oval and produced as short lobes in front of median lanceolate adductors, but not surrounding them.

Dorsal interior with massively calcified cardinalia 21% as long as the brachial valve and 34% as wide as the valve length; brachiophores widely divergent and with weakly divergent bases which are often masked by thick secondary shell deposition to form thick triangular pads ankylosed to median ridge by thick ancillary struts in the form of a straight bar; inner faces of brachiophores with pits; cardinal process with thick shaft continuous with posterior end of median ridge, myophore bilobed and posteriorly crenulated, filling notothyrium and projecting slightly beyond hinge line; adductor muscle field subquadrate, raised on shallow platform and with smaller posterior elements, divided by median ridge and extending anteriorly for 52% of length of the brachial valve.

MATERIAL AND LOCALITIES. Lectotype (Figs 316–7) BB 24077 (selected Cocks 1978 : 66), length 6·8 mm, width 8·6 mm, from loc. 50; also (colln O35) Fig. 320, BB 72458, length 4·1 mm, width 4·8 mm; Fig. 321, BB 72457, length 9·9 mm, width 12·8 mm; Fig. 323, BB 72456, est. length 10·5 mm, width 15·0 mm; Fig. 324, BB 72455, length 7·4 mm, width 8·9 mm; Fig. 328, BB 72459, length 8·4 mm, width 10·4 mm; Fig. 329, BB 72463, length 5·2 mm, width 6·8 mm; Fig. 330, BB 72462, length 11·4 mm, width 13·8 mm; Fig. 335, BB 72460, length 9·1 mm, width 12·6 mm. Lectotype of *inconstans* (Figs 318–9) BB 10259, length 11·1 mm, width 12·3 mm, from loc. 49, also (colln O98) Fig. 322, BB 72448; Fig. 325, BB 72450; Fig. 326, BB 72447; Fig. 327, BB 72449; Figs 331–4, BB 72451–4, also in the Onny Shale Formation.

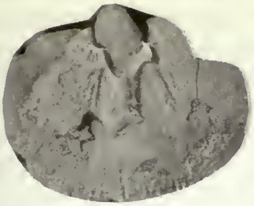
DISCUSSION. See p. 261.

Onniella depressa Bancroft
Figs 294–315

1945 *Onniella depressa* Bancroft : 218–221; pl. 30, figs 10–13.
1945 *Onniella sinuata* Bancroft : 222; pl. 30, figs 14–15.

DESCRIPTION (emended). Subcircular to subquadrate unequally biconvex *Onniella*, with evenly

Figs 306–331 *Onniella depressa* Bancroft, internal and external moulds of brachial valves: 306 = BB 72442, ×2·5, 307 = BB 72438, ×2·5, 308 = BB 72465, ×3, 309 = BB 72440, ×3, 310 = BB 72446, ×3, 311 = BB 72464, ×2·5, 312 = BB 72436, ×2·5, 313 = BB 72439, ×2·5, 314 = BB 72445, ×2·5, 315 = BB 72437, ×2·5. *Onniella broeggeri* Bancroft, conjoined valves: 316–7 = pedicle and brachial views respectively of lectotype BB 24077, ×2·5, 318–9 = pedicle and brachial views respectively of BB 10259 (lectotype of synonymized *O. inconstans*), ×1·5; internal moulds of brachial valves: 320 = BB 72458, ×5, 321 = BB 72457, ×2·5, 322 = BB 72448, ×2·5, 323 = BB 72456, ×2·5, 324 = BB 72455, ×3, 325 = BB 72450, ×2·5, 326 = BB 72447, ×2·5, 327 = BB 72449, ×2·5; internal moulds of pedicle valves: 328 = BB 72459, ×2·5, 329 = BB 72463, ×4, 330 = BB 72462, ×2·5, 331 = BB 72454, ×2·5.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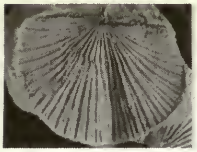
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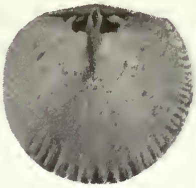
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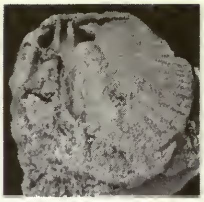
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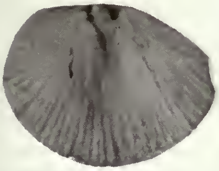
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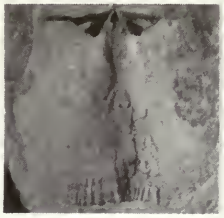
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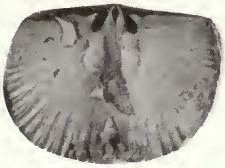
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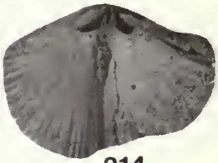
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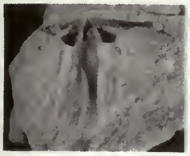
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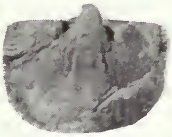
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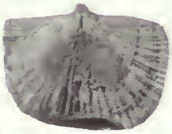
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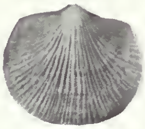
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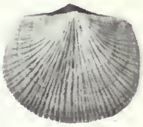
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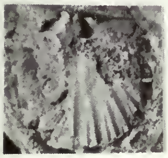
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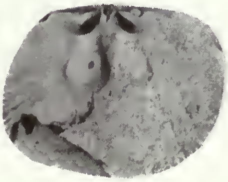
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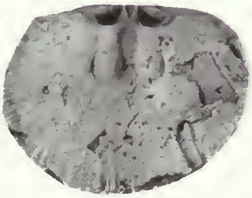
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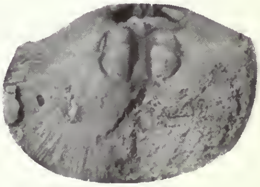
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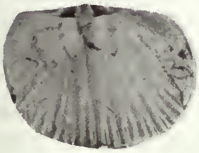
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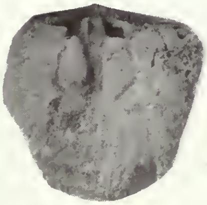
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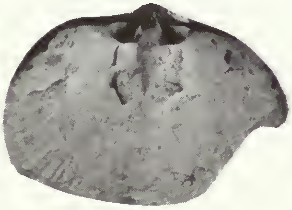
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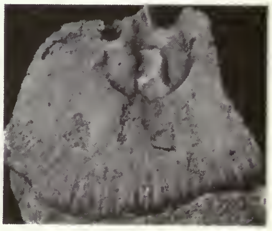
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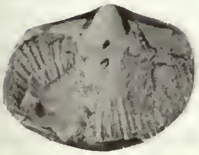
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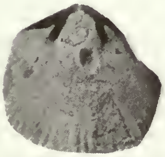
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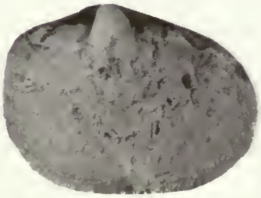
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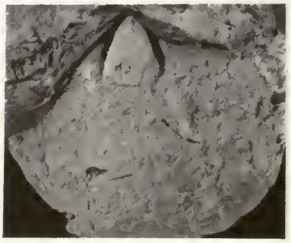


convex, deeply sulcate brachial valve 79% as long as wide, and a pedicle valve 83% as long as wide and 34% as deep as long; dorsal interarea short, slightly curved, anacline, notothyrium open; ventral interarea short, curved, apscaline, delthyrium open; radial ornamentation commonly 6 costellae per mm, 2 mm anterior of dorsal umbo, branching freely developed.

Ventral interior with massive teeth supported by subparallel dental lamellae which extend anteriorly for 23% of the length of the valve and have weak or moderately strong crural fossettes on their inner faces; adult ventral muscle field angular cordate to subpentagonal and extending anteriorly for 35% the length of the pedicle valve, maximum width 32% of the valve length; elongate oval diductor lobes do not surround median lanceolate adductor scar.

Dorsal interior with massive cardinalia 18% as long as the brachial valve and 34% as wide as the valve length; brachiophores slightly divergent with weakly divergent bases, commonly expanded by secondary shell deposition to form thick triangular pads ankylosed to median ridge by ancillary struts; inner faces of brachiophore with pits; cardinal process with thick shaft posteriorly bilobed and crenulated, filling notothyrium and projecting slightly beyond hinge line; adductor scar subquadrate with smaller posterior elements, divided by median ridge and extending anteriorly for 48% the length of the brachial valve.

MATERIAL AND LOCALITIES. Lectotype (Figs 296–7) BB 10251 (selected Cocks 1978 : 66), length 12·7 mm, width 14·8 mm, from loc. 37, also (colln O24) Fig. 298, BB 72435, length 5·2 mm, width 6·8 mm; Fig. 300, BB 72434, length 7·8 mm, width 10·0 mm; Fig. 302, BB 72433, length 13·5 mm, width 16·8 mm; Fig. 307, BB 72438, length 7·1 mm, width 9·4 mm; Fig. 312, BB 72436, length 10·6 mm, est. width 11·0 mm; Fig. 315, BB 72437. Lectotype for *sinuata* Figs 294–5, BB 10254, length 10·7 mm, width 11·8 mm, from loc. 40. From loc. 41, colln O104, Fig. 310, BB 72446, Fig. 314, BB 72445; also colln O105, Fig. 301, BB 72444, Figs 304–6, BB 72441–3, Fig. 309, BB 72440, Fig. 313, BB 72439. From loc. 44, colln OA29, Fig. 299, BB 72466, Fig. 308, BB 72465, Fig. 311, BB 72464, also colln OA30, Fig. 303, BB 73679, length 11·6 mm, width 14·3 mm. Also recorded from locs 36, 38 and 39, all in the Acton Scott Formation.

DISCUSSION. See p. 261.

Onniella reuschi Bancroft
Figs 268–293

1928*a* *Onniella reuschi* Bancroft : 57–58; pl. 2, figs 10–13.
1945 *Onniella reuschi* Bancroft; Bancroft : 215–217; pl. 29, figs 1–6; pl. 30, figs 1–3.
1945 *Onniella grandis* Bancroft : 217; pl. 29, figs 7, 8, 14; pl. 30, figs 4–6.
1945 *Onniella aspasia* Bancroft : 217–218; pl. 29, figs 10–12; pl. 30, figs 7–9.
1958 *Onniella reuschi* Bancroft; Dean : pl. 25, figs 5–6.
1963 *Onniella grandis* Bancroft; Williams & Wright : pl. 1, figs 1, 5, 8; pl. 2, fig. 5.

DESCRIPTION (emended). Large, subcircular unequally biconvex *Onniella*, with evenly convex weakly sulcate brachial valve 74% as long as wide and about one-ninth as deep as long, and a pedicle valve 80% as long as wide and 22% as deep as long; dorsal interarea short, straight, anacline, notothyrium open; ventral interarea short, curved, apscaline, delthyrium open; radial ornamentation commonly 7 costellae per mm, 2 mm anterior of dorsal umbo, internal branching predominantly developed in sectors I to IV.

Ventral interior with strong, massive teeth supported by divergent dental plates which extend anteriorly for 19% of the length of the valve and have very weak crural fossettes on their inner faces; adult ventral muscle field rounded cordate and extending anteriorly for 34% the length of the pedicle valve, maximum width 31% of the valve length; oval diductor lobes do not surround median lanceolate adductor scar.

Dorsal interior with massive subparallel brachiophores which extend anteriorly for 17% of the valve length and splay laterally for 31% of the valve length; brachiophore secondarily thickened and with divergent bases; ancillary struts strong; cardinal process consisting of thick shaft posteriorly continuous with median ridge and with massive, ovoid, posteriorly crenulated, bilobed myophore, completely filling notothyrium and projecting slightly posterior of hinge line; thick median ridge divides poorly-impressed adductor scars which extend anteriorly for 47% of the length of the valve.

MATERIAL AND LOCALITIES. Lectotype BB 10236 (selected Cocks 1978 : 66), length 8·2 mm, width 10·9 mm, from loc. 25, as is Fig. 283, BB 72408, length 12·7 mm, width 17·6 mm (colln WFT7). Also loc. 28, collns M10 and M11, including Figs 268–271, BB 72412–5, Figs 282, 284, 293, BB 72409–11. Loc. 46, Fig. 281, BB 10239 (lectotype of *grandis*, length 13·8 mm, width 17·0 mm) also (colln AS5) Figs 272, 273, 280, 285–7, BB 72417–22. Loc. 35, Fig. 274, BB 10248 (lectotype of *aspasia*, length 13·8 mm, width 17·0 mm) and colln DH1, Figs 275–7, 288–290, BB 72423–8. Loc. 47, colln CF4, Figs 278–9, 291–2, BB 72429–32. Also recorded from locs 22, 33–5, 43–5.

DISCUSSION. *Onniella* is abundant in the uppermost Crosspipes Member, Acton Scott Formation and Onny Shale Formation. Bancroft (1928*a* : 56–57) erected two species from the Upper Caradoc, *O. reuschi* and *O. broeggeri*, the latter of which he designated 'genotype'. He subsequently (1945 : 211–222) erected a series of seven species (five of them new) which, arranged in stratigraphical order, are *O. reuschi*, *O. grandis*, *O. aspasia*, *O. depressa*, *O. sinuata*, *O. inconstans* and *O. broeggeri*. He considered there to be two phylogenetic groups (1945 : 215), firstly the group of *O. grandis* forms, which encompassed *O. reuschi*, *O. grandis*, *O. aspasia*, *O. depressa* and *O. inconstans*. Bancroft claimed this group exhibited multiple progressive trends which were continuous and unidirectional. *O. aspasia* and *O. inconstans* were considered to be slightly divergent from the main lines of descent. The second group was that of *O. broeggeri*, which also includes *O. sinuata*.

Distinction between the seven species and the two species groups he drew in terms of shell size (an unreliable feature owing to transport and other environmental controls), impression of muscle scars, ribbing densities and relative branching of internal and external costellae. As pointed out by Williams & Wright (1963) and Williams (1963), in Bancroft's study of *Howellites* he did not subject his data to tests of significance, so that chosen characters, particularly rib patterns, used for specific diagnosis may not have been as sufficiently different as he believed and thus so reliable taxonomically. Bancroft also erected some species of *Onniella* on only a limited amount of material and often with little knowledge of the internal structures and variation. For example, he erected *O. sinuata* on a small number of conjoined valves and only one dorsal interior; apparently he had no ventral interiors.

For the present study large collections of topotypic material were obtained, as well as accessory populations (e.g. colln M11 corresponds to the cotype material used by Bancroft in describing *O. reuschi*, colln CF4 is an Actonian population of *O. reuschi* and colln O33 is stratigraphically the highest population of any *Onniella* in the Caradoc area and is assigned to *O. broeggeri*). The statistical data given in Tables 74–82 are based on these collections.

As regards bivariate statistics, species were arranged in stratigraphical order and each population tested against those adjacent. The topotype population (WFT7), cotype population (M11) and colln CF4 do not differ from each other in bivariate or other characters and are treated as the species *O. reuschi*. Also population O33 does not differ from topotype *O. broeggeri*.

O. reuschi (WFT7) differs from *O. grandis* solely in having a slower increase in width of the dorsal cardinalia ($P < 0{\cdot}05$), yet *O. grandis* and *O. aspasia*, *O. reuschi* (WFT7) and *O. aspasia* do not differ as regards bivariate characteristics. *O. reuschi* differs from *O. depressa* in having a relatively narrower brachial valve ($P < 0{\cdot}05$) and a slower increase in length of the dorsal cardinalia ($P < 0{\cdot}05$). However, *O. reuschi* and *O. depressa* do not differ from *O. inconstans*, which itself does not differ from *O. reuschi* (WFT7) or *O. broeggeri*. Further, *O. broeggeri* does not differ from the topotype or cotype populations of *O. reuschi*, or from the Actonian population CF4.

In summary, bivariate statistics show that the seven 'species' of *Onniella* are very similar morphologically and do not segregate into neat species patterns. Thus it is misleading for Bancroft (1945) to distinguish

1. *O. reuschi* from *O. grandis* in terms of the greater size and larger muscle field of the latter
2. *O. aspasia* from *O. grandis* in terms of the delicate nature of the crural plates and smaller dorsal muscle area of the former

3. *O. depressa* from the remaining species by its relatively long shell and rounded contour
4. *O. broeggeri* by its small size, and
5. *O. inconstans* by the characteristic form of the valves.

Although the length/width relationship of the adult ventral muscle field (in valves above 4 mm in length) does not change relative proportions from species to species, the actual configuration of the scar does show changes of shape. There are two basic ventral muscle field configurations, here referred to as 'U'- and 'V'-shaped (Fig. 352). Table 83 lists the distribution of pedicle valves with the various muscle field shapes, from the topotype populations. Chi-squared (χ^2) tests show there to be three morphological groups in which the component species do not differ significantly:

1. *O. reuschi*, *O. grandis* and *O. aspasia*
2. *O. depressa* and *O. sinuata*
3. *O. inconstans* and *O. broeggeri*

All three species of Group 1 have predominantly U-shaped muscle fields and differ significantly ($P < 0{\cdot}05$) from both species of Group 2, which have approximately equal U- and V-shaped muscle fields. They also differ from both species of Group 3 ($P < 0{\cdot}01$), which have a predominantly V-shaped muscle field. Both species of Group 2 differ from both Group 3 species ($P < 0{\cdot}05$).

Strength of the crural fossettes varies amongst the seven 'species'. On specimens above 4 mm in length these have been categorized as absent, weak or strong. The distributions for the topotype populations are shown in Table 84. Chi-squared (χ^2) tests again define the same three groups, with the component species not significantly different. All species of Group 1 differ from Group 2 and 3 species ($P < 0{\cdot}01$ in each case) in having weak or absent crural fossettes. Group 2 species, with strong or weak crural fossettes, differ significantly from Group 3 species ($P < 0{\cdot}01$), which have predominantly strong crural fossettes.

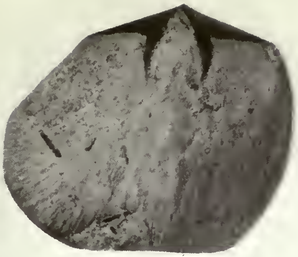
As noted by Bancroft (1945), the impression of the dorsal muscle field of *Onniella* varies. Table 85 lists the distribution of brachial valves with strongly or weakly impressed dorsal adductor scar. The following two groups are evident, in which the component species do not differ significantly:

1. *O. reuschi*, *O. grandis*, *O. aspasia*, *O. depressa* and *O. sinuata*
2. *O. inconstans* and *O. broeggeri*

Group 1 species, with a weakly-impressed dorsal adductor scar, differ significantly from Group 2 species ($P < 0{\cdot}01$), which have a strongly-impressed adductor scar.

Bancroft mainly defined *Onniella* species on their ribbing patterns. Consequently, costellae densities as well as costellae insertions have been analysed (see Tables 86, 87). For costellae densities data were grouped into 5/6 and 7/8 costellae and tested for significance. *O. reuschi*, *O. aspasia* and *O. grandis* do not differ significantly. The former two have slightly finer ribbing and differ significantly ($P < 0{\cdot}05$) from the slightly coarser-ribbed *O. depressa* and *O. sinuata*, which themselves are similar and also do not differ significantly from *O. inconstans* and *O. broeggeri*. *O. grandis* does not differ significantly from any species. In conclusion, although there is a general trend for finer-ribbed species to occur in the top of the Cheney Longville Formation (i.e. *O. reuschi*) and lower Acton Scott Formation (i.e. *O. grandis* and *O. aspasia*), and for coarser-ribbed species to occur in the upper Acton Scott Formation (i.e. *O. depressa* and *O. sinuata*) and Onny Shale Formation (i.e. *O. inconstans* and *O. broeggeri*), much of the variation is not significant.

Figs 332–351 *Onniella broeggeri* Bancroft, internal moulds of pedicle valves: 332 = BB 72451, ×2·5, 333 = BB 72452, ×2·5, 334 = BB 72453, ×2·5, 335 = BB 72460, ×2·5. *Horderleyella* cf. *plicata* Bancroft, internal moulds of pedicle valves: 336 = BB 72492, ×2·5, 337 = BB 72493, ×1·2; internal and external moulds of brachial valves: 338 = BB 72494, ×1·4, 339 = BB 72495a, ×1·2, 340 = BB 72495b, ×0·9. *Reuschella bilobata* (J. de C. Sowerby), internal moulds of pedicle valves: 341 = BB 9269 (lectotype of synonymized *R. semiglobata*), ×1·5, 342 = BB 72508, ×1, 343 = BB 72509, ×0·9, 344 = BB 72507, ×0·9; internal and external moulds of brachial valves: 345 = BB 72505, ×1·1, 346 = BB 72506, ×1, 347 = BB 72504b, ×1·3, 348 = BB 72504a, ×2, 349 = BB 72503, ×0·9. Internal mould of pedicle valve of *Triplesia* sp.: 350 = BB 72370, ×3. Internal mould of pedicle valve of *Bicuspina* sp.: 351 = BB 72371, ×3.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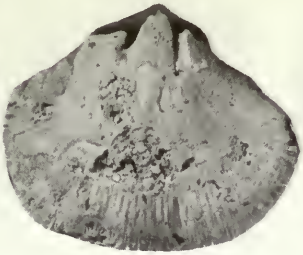
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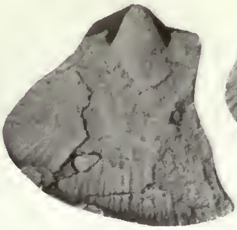
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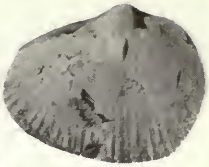
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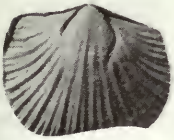
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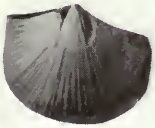
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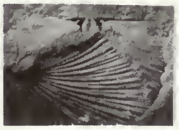
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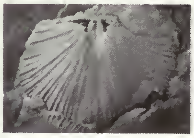
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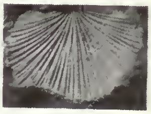
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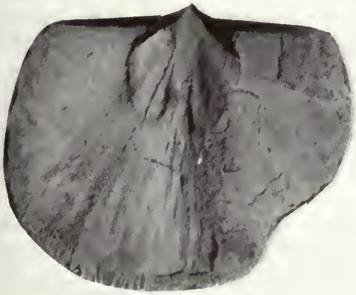
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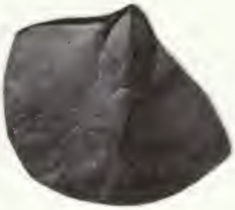
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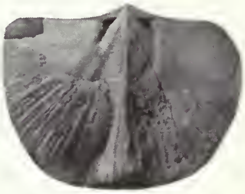
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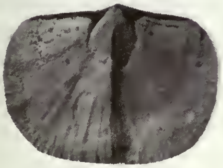
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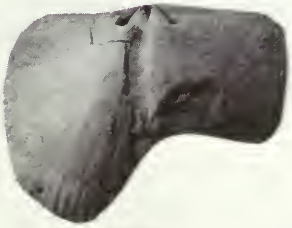
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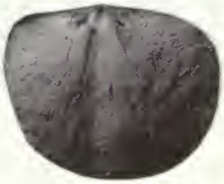
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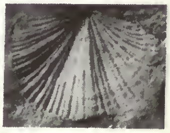
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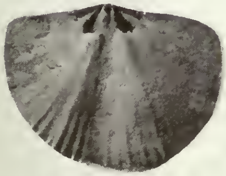
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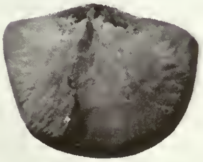
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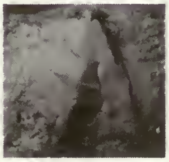
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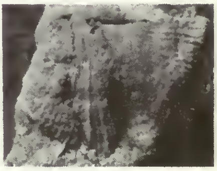
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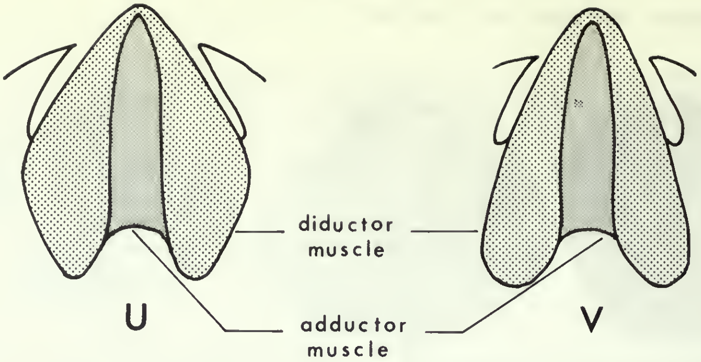


Fig. 352 Diagrammatic representation of the U- and V-shaped pedicle muscle fields of *Onniella*.

The earlier insertion of eight costellae relative to eight others has been analysed (Table 87); the data for *O. broeggeri* are from Williams (1963 : 408). 1b̄)1å are constantly fairly evenly associated throughout all seven 'species'. With regard to the earlier insertion of 2b̄)2å, both *O. depressa* and *O. sinuata* are similar and differ significantly ($P < 0{\cdot}05$) from the remaining species in the earlier insertion of 2å. *O. inconstans* and *O. broeggeri* have similar insertion rates for 2ā1̄)2b̄ and differ significantly ($P < 0{\cdot}05$) from the remaining species in the earlier insertion of 2b̄. Rib patterns 3ā1̄ā)3å and 3ā1̄ā)2å are constant throughout all seven species, with the earlier insertion of 3å and 2å respectively. 3å is also regularly inserted earlier than 3c̄ in all seven species. Regarding 3ā1̊)2b̄1̄, *O. depressa* and *O. sinuata* have similar insertion rates, but in having the earlier insertion of 3ā1̊ differ significantly from the remaining species ($P < 0{\cdot}05$–$0{\cdot}01$). With the insertion of 4b̄)4b̊ *O. inconstans* and *O. broeggeri* are similar, yet significantly differ ($P < 0{\cdot}001$) from the remaining species in the earlier insertion of 4b̊.

In summary, *O. reuschi*, *O. grandis* and *O. aspasia* are conspecific, as are *O. depressa*/*O. sinuata* and *O. inconstans*/*O. broeggeri*. Consequently, three species are recognized, *O. reuschi*, *O. depressa* and *O. broeggeri*. They differ in the configuration of the ventral muscle field and the strength of the crural fossettes. Further, *O. broeggeri* can be distinguished by its more heavily impressed quadripartite dorsal adductor muscle field, the significantly earlier insertion of both 2b̄ relative to 2ā1̄ and 4b̊ relative to 4b̄. *O. depressa* can be further distinguished by the significantly earlier insertion of 2å relative to 2b̄ and 3ā1̊ relative to 2b̄1̄. *O. reuschi* tends to have the finest ribbing although the distribution within a population is not significantly different from *O. depressa* and *O. broeggeri*.

Family **HARKNESSELLIDAE** Bancroft, 1928

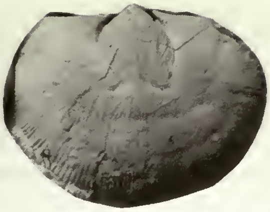
Genus ***HORDERLEYELLA*** Bancroft, 1928

Horderleyella cf. ***plicata*** Bancroft

Figs 336–340

1928*b* *Horderleyella plicata* Bancroft : 186–187; pl. 1, figs 15–18.

Figs 353–378 *Heterorthina notata* (Barrande), internal moulds of pedicle valves: 353 = BB 72342, ×1·6, 354 = BB 72341, ×1·6, 355 = BB 72346, ×1·6, 356 = BB 73683, ×1·8, 357 = BB 73684, ×1·8, 358 = BB 72345, ×2·1, 359 = BB 72343, ×1·6, 360 = BB 72344, ×1·8; internal and external moulds of brachial valves: 361 = BB 72340, ×1·7, 362 = BB 72347, ×2·2, 363 = BB 72337, ×1·5, 364 = BB 72338, ×1·2, 365 = BB 72339, ×1·1, 366 = BB 73682, ×1·3. *Heterorthina praeculta* Bancroft, internal moulds of pedicle valves: 367 = BB 72284, ×1·3, 368 = BB 72285, ×1·5, 369 = BB 72286, ×1, 370 = BB 72287, ×1·2; internal and external moulds of brachial valves: 371 = BB 72288a, ×1·6, 372 = BB 72288b, ×1·2, 373 = 72291a, ×1·2, 374 = BB 72291b, ×1·2, 375 = BB 72289b, ×1·3, 376 = BB 72289a, ×1·8, 377 = BB 72290b, ×1·1, 378 = BB 72290a, ×1·3.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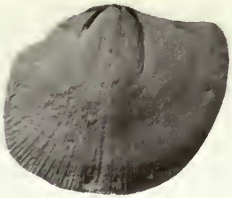
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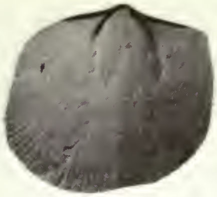
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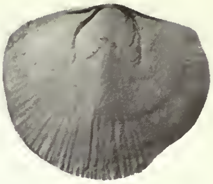
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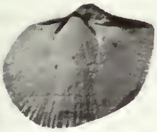
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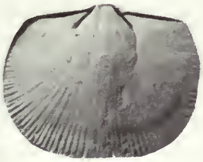
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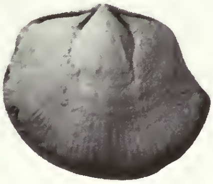
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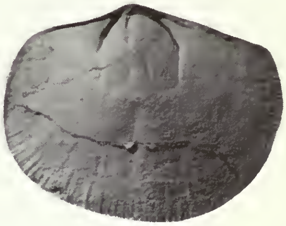
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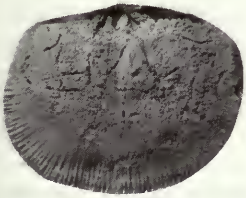
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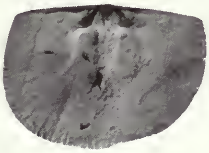
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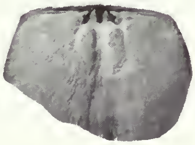
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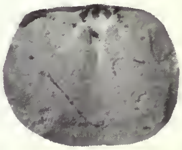
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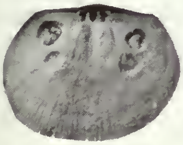
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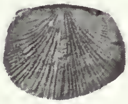
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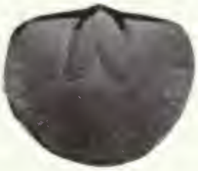
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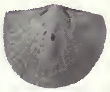
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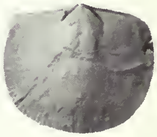
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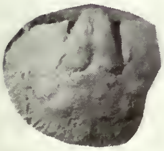
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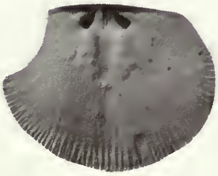
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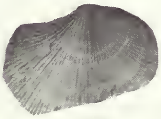
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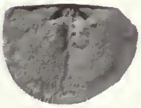
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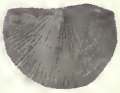
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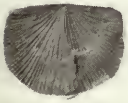
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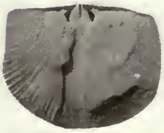
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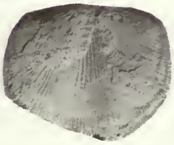
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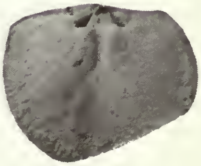
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1945 *Horderleyella plicata* Bancroft : 236–237; pl. 31, figs 4–7; pl. 32, figs 1–4.
1974 *Horderleyella* cf. *plicata* Bancroft; Williams : 102–103; pl. 16, figs 17, 19, 20; pl. 17, fig. 1.

DESCRIPTION. Ventribiconvex *Horderleyella* with right-angled cardinal margins, brachial valve approximately seven-tenths as long as wide and one-fifth as deep as long, pedicle valve three-quarters as long as wide and up to one-third as deep as long, and varying from weakly convex carinate forms to strongly convex non-carinate forms, ventral interarea long, slightly curved apscaline, delthyrium open, dorsal interarea short flat anacline, notothyrium open; radial ornamentation fascicostellate and ornamented by 4 or 5 fascicostellae per mm, 2 mm anteromedially of the dorsal umbo.

Ventral interior with small teeth and weak crural fossettes, supported by short divergent dental lamellae which extend anteriorly for one-seventh the valve length and extend forward as fairly strong ridges peripheral to the muscle field and curving back to the mid-line; ventral muscle scar bilobed, one-third as long as the valve and one-fifth as wide as the valve is long, and consisting of a narrow, elongately oval median adductor impression not enclosed by triangular diductor tracks.

Dorsal interior with cardinal process consisting of short, slender shaft expanding anteriorly for one-sixth the valve length and splaying laterally for one-quarter of the length of the valve, fulcral plates defining sockets; muscle field obscure.

DIMENSIONS.	length	width
Internal mould of pedicle valve, BB 72492	7·3 (est.)	8·9 (est.)
Internal mould of pedicle valve, BB 72493	14·2	16·8
Internal mould of brachial valve, BB 72494	10·5 (est.)	14·2
Internal and external mould of brachial valve, BB 72495a, b	13·0	17·6

HORIZON AND LOCALITIES. BB 72492 from colln H, loc. 31. BB 72493, BB 72494 and BB 72495,a b from colln M11, loc. 28.

DISCUSSION. A small number of moulds recovered from the Crosspipes Member (Marshbrookian) appear to be conspecific with *H. plicata* Bancroft from the Costonian and Harnagian of the type Caradoc. *H. plicata* may possibly be slightly coarser ribbed, but that aside this stock appears to have undergone little morphological change through the period Costonian–Marshbrookian.

Genus ***REUSCHELLA*** Bancroft, 1928

TYPE SPECIES. *Reuschella semiglobata* Bancroft by original designation of Bancroft (1928*b* : 180), treated here as a junior subjective synonym of *Orthis bilobata* J. de C. Sowerby.

Reuschella bilobata (J. de C. Sowerby)
Figs 341–349

1839 *Orthis bilobata* J. de C. Sowerby *in* Murchison : 640; pl. 19, fig. 7.
1869 *Orthis vespertilio* J. de C. Sowerby; Davidson : 236 *pars*; pl. 30, figs 11, 17, 18, *non* figs 12–16.
1928*b* *Reuschella semiglobata* Bancroft : 188–190; pl. 2, figs 9–12.
1945 *Reuschella bilobata* (J. de C. Sowerby) Bancroft : 239.

DESCRIPTION. Strongly dorsibiconvex subquadrate *Reuschella* with rounded cardinal margins, brachial valve approximately three-quarters as long as wide and one-third as deep as long with a very shallow sinus, pedicle valve slightly concave in cross-section parallel to hinge and approximately three-quarters as long as wide and with a mean depth relative to length of one-eighth at the sharp median carina, lateral folds undulate; ventral interarea long, curved apscaline, delthyrium open, dorsal interarea short, flat anacline and with open notothyrium; radial ornamentation medium to coarsely fascicostellate.

Ventral interior with massive teeth and supported by divergent to subparallel dental plates which extend anteriorly for one-quarter the valve length and extend forward as strong ridges peripheral to muscle field; ventral muscle scar bilobed, two-fifths as long as valve and one-third as wide as valve length, and consisting of a narrow lanceolate median adductor impression not enclosed by elongate triangular diductor tracks.

Dorsal interior with cardinal process consisting of massive rounded shaft and crenulated, ridged bulbous myophore completely filling notothyrium, notothyrial platform massive and indented anteriorly by moderately deep pits of adductor muscle scar, brachiophores divergent, extending anteriorly for one-seventh of the valve length and splaying laterally for one-third of the valve length, sockets deep and crenulated, muscle scar obscure.

Material and localities. Lectotype (selected Cocks 1978 : 76) GSM Geol. Soc. Colln GSd 5527, from Acton Scott Formation, 'Acton Scott' (exact locality unknown). Lectotype of *semiglobata* (Fig. 341) BB 9269, length 25·7 mm, width 31·0 mm, from loc. 42. Loc. 24, colln WFT1, e.g. Fig. 349, BB 72503, length 24·4 mm, width 29·5 mm; also colln WFT2, e.g. Figs 347–8, BB 72504, length 11·4 mm, width 15·0 mm. Loc. 1, colln CL7, e.g. Fig. 342, BB 72508, length 25·1 mm, width 33·3 mm. Loc. 44, colln OA25, e.g. Fig. 345, BB 72505, length 23·8 mm, width 36·2 mm. BB 72509 (Fig. 343), BB 72507 (Fig. 344) and BB 72506 (Fig. 346) are with no precise locality labels, but are probably from loc. 47. Known from locs 1–48.

Discussion. *Reuschella* occurs throughout the Alternata Limestone to Acton Scott Formation but never in any abundance. J. de C. Sowerby *in* Murchison (1839) described *Orthis bilobata* from some part of this sequence. Bancroft (1928*b*), when he erected *Reuschella*, commented on the fact that *O. bilobata* belonged to *Reuschella*, but because it was not precisely located and known only by the interior of the brachial valve he ignored it. Instead, he erected *R. semiglobata*, saying it differed from *R. bilobata* in having small wings, a more conspicuous sinus in the brachial valve, absence of well-defined dorsal muscle scars and in having a greater longitudinal extension of the crural plates.

New collections, and examination of Bancroft's type material, show *R. semiglobata* to be a variable stock within which is encompassed the single figured specimen of *R. bilobata*. Thus *R. semiglobata* is treated as a synonym of *R. bilobata*. Further, all post-Lower Longvillian *Reuschella* specimens are assigned to *R. bilobata*.

Bancroft (1928*b*) described *R. horderleyensis* from pre-Upper Longvillian strata, in the type Caradoc. He did, however, note that in terms of shell shape some *R. horderleyensis* specimens are comparable to *R. bilobata*. However, until more is known of the variability of *R. bilobata* the two species are best kept separate.

Family **HETERORTHIDAE** Schuchert & Cooper, 1931

Genus ***HETERORTHIS*** Hall & Clarke, 1892

Heterorthis alternata (J. de C. Sowerby)

1839 *Orthis alternata* J. de C. Sowerby *in* Murchison : 638; pl. 19, fig. 6.
1871 *Orthis alternata* J. de C. Sowerby; Davidson : 264 *pars*; pl. 31, figs 7–8, *non* figs 1–6.
1963 *Heterorthis alternata* (J. de C. Sowerby) Williams : 418; pl. 9, figs 1–6, 8, 9.

Williams (1963) has redescribed and figured this species, and his work will not be duplicated here. The species occurs at locs 1–8 inclusive and 44. Further, Dean (1958) reported a thin shell bed of *H. alternata* in the lowest Acton Scott Formation of the Onny Valley, but this is not now exposed, and Harper (1978) another thin shell bed in the Onny Shale Formation.

Genus ***HETERORTHINA*** Hall & Clarke, 1892

1928*a* *Heterorthina* Bancroft : 59.
1960 *Elsaella* Alichova : 192.
1975 *Elsaella* Alichova; Hints : 78.

Diagnosis. Transverse, very gently and unequally biconvex heterorthids with more deeply convex pedicle valve and shallow, persistently sulcate brachial valve; ventral interarea short, curved, apscaline with open delthyrium; dorsal interarea short, anacline; notothyrium completely filled by cardinal process; shell punctate; radial ornamentation multicostellate, of fine to very fine costellae with both external and internal branches freely developed in all sectors; costellae curving in posterior regions of shell to intersect hinge line.

Ventral interior with small teeth supported by short, blunt, divergent dental lamellae; pedicle callist well developed; muscle field large, elongately pentagonal, occasionally with semiflabellate diductor tracks, anteriorly not enclosing lanceolate adductor scar (very rarely anterior lobes of convergent diductor scars meet medially to surround adductor scars completely.)

Dorsal interior with strong cardinal process, anterior shaft with cleft, myophore expanded into large ovoid structure which early in ontogeny is bilobed but which with maturity develops up to four small septa dividing myophore into separate lobes; posterior end of myophore crenulated and extending well beyond hinge line; brachiophores greatly divergent, with divergent bases, fulcral plates absent; dorsal adductor scars elongate with approximately equal posterior and anterior elements.

TYPE SPECIES. *Heterorthina praeculta* Bancroft, by original designation of Bancroft (1928*a* : 59).

DISCUSSION. Bancroft (1928*a* : 59–60) erected this genus; whilst recognizing it was distinct from *Heterorthis alternata* (Sowerby) he noted that it shared many characteristics.

The assignment of *Heterorthina* to a suprageneric category was formerly unsettled. Williams & Wright (1963) placed it in the Dalmanellidae. Later Harper, Boucot & Walmsley (1969) questionably assigned the genus to the subfamily Heterorthinae Schuchert & Cooper, of the Rhipidomellidae Schuchert, 1913. It is now clear from the thorough work of Havlíček (1970) that *Heterorthina* should unquestionably be assigned to the Heterorthidae of Schuchert & Cooper, 1931. The diverging brachiophore bases and lobation of the cardinal process myophore into a bilobed, trilobed or quadrilobed structure suggest strong affinities with *Tafilaltia* Havlíček, 1970 and *Svobodaina* Havlíček, 1950. The configuration of the pedicle valve muscle field of *Heterorthina* also suggests such affinities. Such a line of derivation involved increasing complexity of the cardinal process myophore and lobation of the pedicle diductor muscle field. It is interesting to note that young specimens of the pedicle valves of *Svobodaina inclyta* (Barrande), figured by Havlíček (1970 : pl. 5), are remarkably similar, especially in diductor muscle scar configuration, to adult *Heterorthina*. Further, Havlíček (1970 : 23) notes that, rarely, the anterior lobes of the adductor scars of *Svobodaina* touch, to surround the adductor tracks completely, a feature also occasionally seen in *Heterorthina praeculta*.

Williams & Wright (1963) placed the genus *Elsaella* Alichova in synonymy with *Heterorthina*. Recently, Hints (1975) has brought *Elsaella* out of synonymy, believing the central position of the pedicle adductor scar, trilobed cardinal process and possibly the rhipidomellid type of ribbing warrant a separate genus. The trilobed cardinal process is common in *Heterorthina* and the central position of the pedicle adductor field is occasionally attained in *H. praeculta* through the medial expansion of the diductor tracks (see also Howe 1965 : text-fig. 6). The only apparent difference between the two genera is the coarser ribbing of *Elsaella*. These small differences do not warrant the retention of the separate genus *Elsaella*.

Heterorthina morgatensis Mélou

1975 *Heterorthina morgatensis* Mélou : 192–203; pl. 20, figs 1–9; pl. 21, figs 1–12; pl. 22, figs 1–5.

DESCRIPTION. Small, transverse, unequally biconvex *Heterorthina*, with weakly convex brachial valve 68 % as long as wide; pedicle valve 71 % as long as wide; delthyrium and notothyrium open, ventral interarea weakly curved apscaline; dorsal interarea short anacline; radial ornamentation of fine costellae 4 or 5 per mm, 5 mm anteromedially of dorsal umbo; costellae in posterior region curving to intersect hinge line.

Ventral muscle field strongly bilobed, flabellate, extending anteriorly for 61 % of the length of the pedicle valve, but not surrounding the median adductor field; diductor scars 58 % as wide as the pedicle valve is long.

Dorsal interior with broad, shallow median ridge, at posterior end of which arises the moderately thick cleft shaft of the cardinal process, which expands into bilobed myophore filling most of the notothyrium; brachiophores divergent, short, strong, with broad divergent bases extending forward for 21% of the length of the brachial valve and splaying laterally for 26% of the valve length; notothyrial platform poorly developed; sockets narrow and well-defined, without fulcral plates; adductor scars elongately oval, impressed quadripartite and extending anteriorly for 50% the length of the valve.

DISCUSSION. See p. 271.

Heterorthina notata (Barrande)

Figs 353–366

1879 *Orthis notata* Barrande : pl. 66, fig. II (*non* pl. 127, fig. VIII).
1932 *Heterorthis barrandei* Schuchert & Cooper : 137.
1950 *Heterorthina notata* (Barrande) Havlíček : 105–106; pl. VIII, figs 1, 2, 8, 10 and 13.
1975 *Heterorthina notata* (Barrande); Mélou : pl. 22, figs 8–9.
1977 *Heterorthina notata notata* (Barrande); Havlíček : 116; pl. 20, figs 18–24.

DESCRIPTION. Transverse, unequally biconvex *Heterorthina*, with evenly weakly convex, shallow sulcate brachial valve 76% as long as wide; pedicle valve 80% as long as wide and 18% as deep as the valve is long; delthyrium and notothyrium open, pedicle callist large, ventral interarea weakly curved apscaline, dorsal interarea short anacline and with prominent growth lines; radial ornamentation of fine costellae commonly 4 per mm, 5 mm anteromedially of the dorsal umbo; costellae curve to intersect hinge line.

Ventral muscle field bilobed with diductor scars, showing well-developed growth increments, extending anteriorly for 42% of the length of the pedicle valve but not surrounding the elongately oval median adductor field; diductor scars 36% as wide as the valve is long; teeth very small, supported by short receding dental plates lacking crural fossettes and extending anteriorly for 15% of the length of the pedicle valve; shell ridge extensions of the dental plates bounding the lateral and anterior parts of the diductor scars.

Dorsal interior with broad median ridge, at posterior end of which arises very broad shaft of cardinal process; myophore extremely large, filling notothyrium, bilobed in individuals below 9 mm in length and trilobed or quadrilobed by septa in more mature specimens, crenulated posteriorly and extending well beyond hinge line; brachiophores divergent, short, very strong and with broad divergent bases, extending forward for 15% of the length of the brachial valve and splaying laterally for 26% of the valve length; notothyrial platform very well developed; well-defined narrow sockets lacking crural fossettes; adductor scars elongately suboval, impressed particularly posteriorly on either side of broad median ridge and extending anteriorly for 48% the length of the valve.

DIMENSIONS.	length	width
Internal mould of brachial valve, BB 72337	14·0	17·0
Internal mould of brachial valve, BB 72338	15·7	20·8
Internal mould of brachial valve, BB 72339	18·0	23·0
Internal mould of brachial valve, BB 72340	16·2	20·0
Internal mould of brachial valve, BB 72347	9·1	12·1
External mould of brachial valve, BB 73682	11·4	13·0
Internal mould of pedicle valve, BB 72341	15·1	19·8
Internal mould of pedicle valve, BB 72342	15·6	21·4
Internal mould of pedicle valve, BB 72343	14·6	17·2
Internal mould of pedicle valve, BB 72344	17·5	20·8
Internal mould of pedicle valve, BB 72345	12·3	15·9
Internal mould of pedicle valve, BB 72346	13·4	18·0
Internal mould of pedicle valve, BB 73683	14·1	16·4
Internal mould of pedicle valve, BB 73684	8·7	11·8

HORIZON AND LOCALITIES. All figured material is from the type locality in a temporary trench along a railway line at Palmovka Hill, Praha – Libeň, Czechoslovakia; Beroun Series, Zahořany Formation.

DISCUSSION. See p. 271.

Heterorthina praeculta Bancroft
Figs 367–379

1928*a* *Heterorthina praeculta* Bancroft : 59–60; pl. 2, figs 14–21.
1963 *Heterorthina praeculta* Bancroft; Williams & Wright : 28; pl. 1, fig. 19.
1965 *Heterorthina praeculta* Bancroft; Wright *in* Williams *et al.*: H335.
1967 *Heterorthina macfarlani* Neuman : A10–A12; pl. 2, figs 1–19.
1975 *Heterorthina praeculta* Bancroft; Mélou : 202; pl. 22, figs 6–7.
1975 *Heterorthina kerfornei* Mélou : 203–207; pl. 23, figs 1–14; pl. 24, figs 1–13.

DESCRIPTION. Transverse, unequally biconvex *Heterorthina* with an evenly weakly convex to flat, weakly sulcate brachial valve 76% as long as wide; pedicle valve 80% as long as wide and 24% as deep as the valve is long; delthyrium and notothyrium open, pedicle callist small, ventral interarea slightly curved apscaline, dorsal interarea short anacline; radial ornamentation of very fine costellae commonly 5 or 6 per mm, 5 mm anteromedially of the dorsal umbo; costellae in posterior region curve to intersect hinge line.

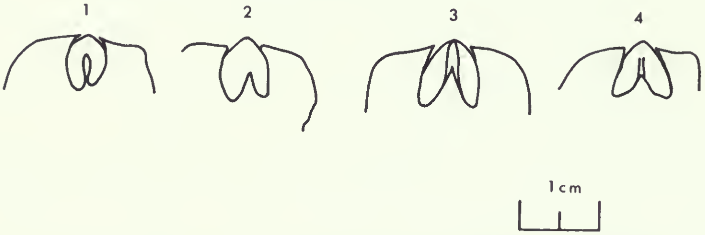


Fig. 379 Range of variation in pedicle musculature of *Heterorthina praeculta*. Note variation from V to U shapes from 1 to 4.

Ventral muscle field bilobed with diductor scars extending anteriorly for 43% of the length of the pedicle valve but not surrounding the elongately oval median adductor scar (rarely adductor scar is surrounded), from which they are separated by shallow depressions (expressed as ridges in mould); diductor scars 39% as wide as the pedicle valve is long; teeth small, supported by short receding dental plates, extending anteriorly for 14% of the length of the pedicle valve and with strong crural fossettes; shallow ridges bound the diductor scars anteriorly.

Dorsal interior with broad median ridge, at posterior end of which arises broad, deeply cleft shaft of cardinal process; myophore large, bilobed or trilobed and crenulated posteriorly extending beyond hinge line; brachiophores short strong, divergent, with broad divergent bases, extending forward for 17% of the length of the brachial valve and splaying laterally for 31% of the length of the valve; sockets narrow, well-defined, without fulcral plates; adductor scars suboval, impressed on either side of median ridge and extending anteriorly for 47% the length of the valve.

MATERIAL AND LOCALITIES. Lectotype BB 9152 (selected Cocks 1978 : 74) from loc. 31, from which also comes all the material figured here, e.g. Fig. 367, BB 72284, length 17·0 mm, width 20·0 mm; Fig. 368, BB 72285, length 9·0 mm, width 10·0 mm; Fig. 369, BB 72286, length 17·0 mm, width 19·8 mm; Fig. 370, BB 72287, length 16·5 mm, width 21·0 mm; Figs 371–2, BB 72288, length 15·3 mm, width 18·6 mm; Figs 373–4, BB 72291, length 10·6 mm, width 13·6 mm; Figs 375–6, BB 72289, length 8·3 mm, width 12·2 mm; Figs 377–8, BB 72290, est. length 17·0 mm, width 20·5 mm. Also recorded from locs 11, 29 and 32.

Outside Britain the species is known from the Grier Limestone Member of the Lexington Limestone (Soudleyan–Longvillian) of North America, and the Schistes de Postolonnec (Caradoc) of Brittany, France.

Discussion. A topotypic sample of *H. praeculta* has been statistically compared with *H. macfarlani* (data given by Neuman 1967 : A11 and Mélou 1975 : 201–202) from the Grier Limestone Member of the Lexington Limestone, U.S.A. (Soudleyan – Longvillian ?), *H. kerfornei* (data given by Mélou 1975 : 205–206) from the Schistes de Postolonnec (Caradoc), France, and *H. morgatensis* (data given by Mélou 1975 : 197–198), also from the Schistes de Postolonnec (Tables 88–96). The comparisons show that *H. macfarlani* and *H. kerfornei* do not differ significantly from *H. praeculta*.

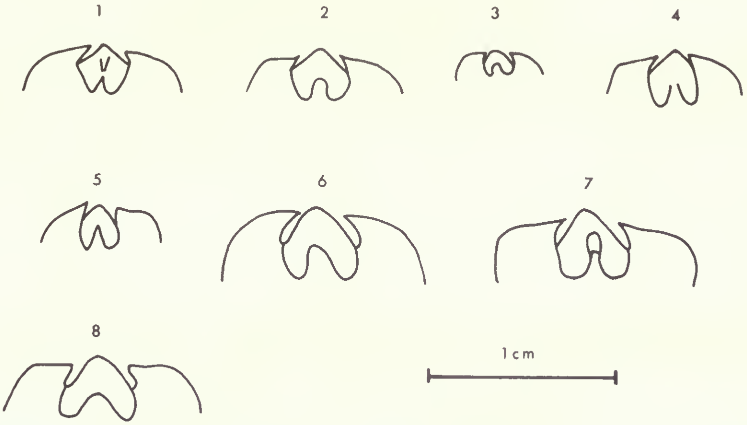


Fig. 380 Range of variation in pedicle musculature of *Heterorthina kerfornei*. Note variation from V to U shapes from 1 to 8.

Mélou (1975 : 206) claims that *H. kerfornei* differs significantly from *H. praeculta* in terms of size, form of the ventral muscle field and morphology of the cardinal process. Absolute size as a taxonomic character is unreliable and the relative dimensions of the ventral muscle fields do not differ significantly. Further, the overall diductor muscle field variation expressed by a population of *H. praeculta* (Fig. 379) is contained within the same variation limits as *H. kerfornei* (Fig. 380). From the figured specimens of *H. kerfornei* populations appear to contain a predominance of individuals which have massive cardinal process shafts filling the notothyrial cavity. In *H. praeculta* the cardinal process shaft is more variable, with individuals having either massive or non-massive ones, and thus *H. kerfornei* populations appear to be end members of the variation of topotype *H. praeculta*. There are therefore no consistent significant morphological differences between *H. praeculta*, *H. macfarlani* and *H. kerfornei*, consequently the relationships between the three species are most conveniently expressed by assuming that they in fact represent a single species, *H. praeculta*.

H. morgatensis differs from *H. praeculta* in the significantly ($P<0{\cdot}005$) faster increase in relative length of the dorsal cardinalia. The dimensions of the ventral muscle field do not differ, yet the diductor tracks of *H. morgatensis* are frequently lobate whereas those of *H. praeculta* are not. Further, the cardinal process of the French species is very strongly bilobate, with a deep groove separating each lobe. From the figured specimens (Mélou 1975 : pl. 21) *H. morgatensis* has 4 (LPB 2798) or 5 (LPB 2800) costellae per mm, 5 mm anteromedially of the dorsal umbo, and so appears more coarsely ribbed than *H. praeculta*.

A topotypic sample of *H. notata* from near Prague differs significantly from *H. praeculta* in the slower relative width of the dorsal cardinalia ($P<0{\cdot}001$), the coarser ribbing (see Table 97; $P<0{\cdot}01$) and in lacking crural fossettes (Table 98; $P<0{\cdot}01$). The pedicle valve diductor tracks show a wide range of variation (Fig. 381) from simple pentagonal scars to exaggerated bilobed tracks, approaching those of *Svobodaina*. *H. notata* differs significantly from *H. morgatensis* in having a slower relative increase in dorsal cardinalia width ($P<0{\cdot}05$), and in having shorter dorsal cardinalia ($P<0{\cdot}05$). The ribbing of the two species approximates, yet the structure of the cardinal process is different.

One of the earliest-described species referred to *Heterorthina*, *H. fairmontensis* (Foerste, 1909 : 322) of Maysville age (Onnian – Pusgillian), appears very similar to *H. praeculta*. Neuman (1967) considered the species to be very similar to *H. macfarlani*. Until more is known about the variation expressed by *H. fairmontensis* the two species are kept separate.

The configuration of the pedicle valve muscle field (i.e. the complete surrounding of the adductor scar by the diductor tracks), the coarse ribbing and the apparent lack of external branches in the first four sectors of ribbing in the brachial valve indicate that the type species of *Elsaella* is probably a distinct species of *Heterorthina*.

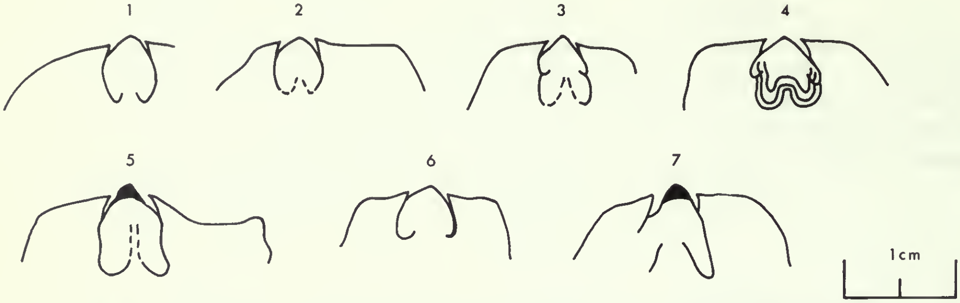


Fig. 381 Range of variation in pedicle musculature of *Heterorthina notata*. Note variation from V to U shapes from 1 to 7.

Genus *MARIONITES* Cooper & Muir-Wood, 1951

DIAGNOSIS (emended). Subcircular heterorthiids with deeply and evenly convex brachial valve with narrow median sulcus, ventral valve weakly resupinate and carinate in transverse profile; radial ornamentation multicostellate with costellae directed posteriorly along hinge line, branching freely developed; ventral interarea short, straight orthocline to very weakly anacline, notothyrium open and filled by massive cardinal process.

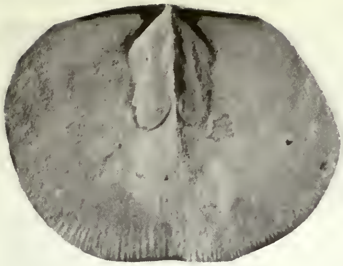
Ventral interior with massive teeth supported by thick, divergent, receding dental lamellae, pedicle callist well developed, muscle field flabellate surrounded by sinuous ridges, with submedian diductor lobes extending beyond, but not completely surrounding, median lanceolate adductor scar.

Dorsal interior with massive, incipiently bilobed cardinal process, brachiophores greatly divergent, brachiophore bases weakly to moderately divergent, notothyrial platform massive, ankylosed to brachiophore bases and extending anteriorly into broad median ridge, weak fulcral plates occasionally developed; dorsal adductor scars elongate with posterior elements deeply inserted into anterior region of notothyrial platform.

TYPE SPECIES. *Marionella typa* Bancroft, by original designation of Cooper & Muir-Wood (1951).

DISCUSSION. The taxonomic position of *Marionites* has been unstable. Bancroft (1928*b*) erected the genus *Marionella* and placed it in a new subfamily, the Harknessellinae, along with the genera *Harknessella* Reed, 1917, *Reuschella* Bancroft, 1928, *Smeathenella* Bancroft, 1928 and *Horderleyella* Bancroft, 1928. He thought that the genus was morphologically intermediate between *Harknessella* and the Rhipidomellidae. Subsequently, Schuchert & Cooper (1932) relegated *Marionella* to a subgenus of *Dinorthis*, a position with which Bancroft apparently agreed (Schuchert & Cooper 1932 : 96). They concluded that despite the lack of information regarding the punctate or impunctate nature of the shell, the internal features suggest dinorthiid affinities. The brachiopod name *Marionella*, being a junior homonym, was replaced by *Marionites* (Cooper & Muir-Wood 1951).

Williams *et al.* (1965) placed *Marionites* in the family Plaesiomyidae Schuchert, 1913, as a subgenus of *Multicostella* Schuchert & Cooper, 1931. The nature of the multicostellate ribbing of *Marionites* (i.e. posteriorly-directed costellae along the hinge line) clearly suggests this genus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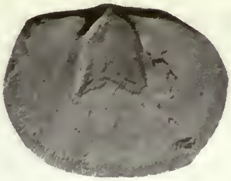
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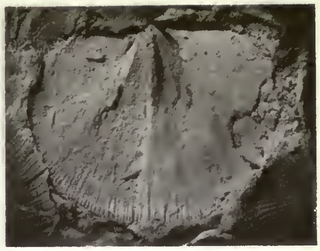
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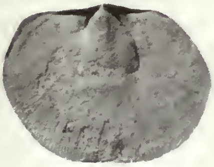
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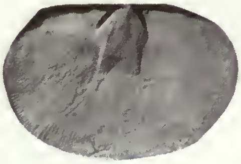
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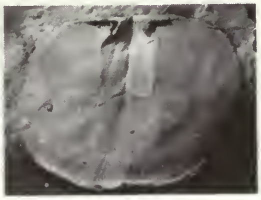
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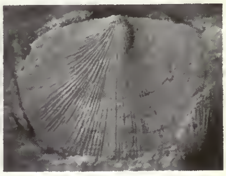
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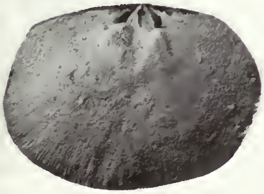
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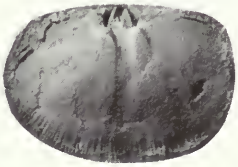
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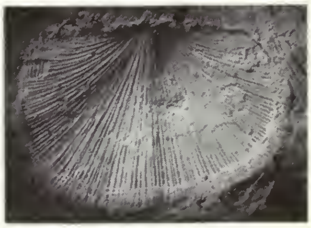
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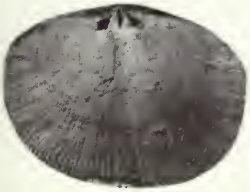
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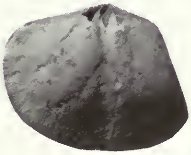
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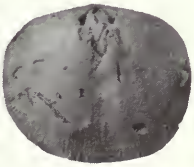
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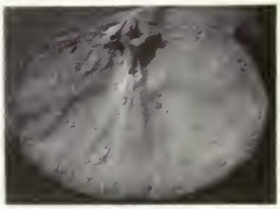
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Figs 382–395 *Marionites typus* (Bancroft), internal moulds of pedicle valves: 382 = lectotype BB 9126, ×2, 383 = BB 72529, ×1·5, 384 = BB 72532, ×2, 385 = BB 72530, ×1·3, 386 = BB 72531, ×1·3; internal and external casts of pedicle valves: 387 = BB 9126, ×1·3, 388 = BB 24626, ×1·3; internal and external moulds of brachial valves: 389 = BB 72537, ×1·6, 390 = BB 24627, ×1·7, 391 = BB 72534b, ×1·9, 392 = BB 72533, ×2·2, 393 = BB 72536, ×1·2, 394 = BB 24628, ×1·2; internal cast of brachial valve: 395 = BB 9124, ×1·1.

belongs in the Heterorthidae of Schuchert & Cooper 1931 (see Havlíček 1970 : 8–9; 1977 : 119). However, as the available material is preserved as internal and external moulds in sandstone, it is not known beyond doubt whether the shell was punctate, although it appears to be very finely so. Further, the nature of the flabellate ventral muscle scar, the massive elliptical cardinal process and brachiophore configuration are all suggestive of heterorthid affinities. None the less, in having a strongly convex brachial valve and resupinate and carinate pedicle valve *Marionites* resembles some members of the Harknessellidae. The similarity between *Marionites* and some genera of the Plaesiomyidae is a clear case of homoeomorphy. Havlíček's (1977) *Marionites* *resupinatus* appears to fall within the variation of *M. typus*, but until this can be adequately demonstrated they are left as separate species.

Marionites typus (Bancroft)
Figs 382–395

1928*b* *Marionella typa* Bancroft : 190–191; pl. 2, figs 13–16.
1932 *Marionella typa* Bancroft; Schuchert & Cooper : pl. 8, figs 16–18.
1951 *Marionites typa* (Bancroft) Cooper & Muir-Wood : 195.
1965 *Marionites typa* (Bancroft); Williams *et al.* : H321, fig. 202, 4a–d.

DESCRIPTION. Subcircular *Marionites* with evenly convex, weakly sulcate brachial valve 12% as long as wide and 28% as deep as long, and resupinate pedicle valve 75% as long as wide; radial ornamentation finely multicostellate, branching freely developed; dental lamellae strong, divergent and extending anteriorly for 15% the length of the pedicle valve, ventral muscle scar extending anteriorly for 49% the length of the valve and 38% as wide as the valve is long; massive cardinalia with divergent brachiophore bases extending anteriorly for 18% of the length of the brachial valve and 28% wide as the valve is long; dorsal adductor scar extending forward of umbo for 45% the length of the valve.

MATERIAL AND LOCALITIES. Lectotype (Figs 382, 387) BB 9126 (selected Cocks 1978 : 51), length 18·0 mm, width 23·5 mm, from loc. 1 (= Bancroft loc. N6). From the same locality came BB 72529 (Fig. 383), length 16·2 mm, width 21·1 mm, BB 72530 (Fig. 385), length 16·8 mm, width 22·3 mm; BB 72531 (Fig. 386), length 15·9 mm, width 24·3 mm; BB 72532 (Fig. 384), length 13·4 mm, width 16·7 mm; BB 72533 (Fig. 392), length 12·0 mm, width 15·3 mm; BB 72534 (Figs 390–1), length 13·5 mm, width 19·1 mm; BB 72535–6 (Figs 393–4); BB 9124 (Fig. 395); BB 24626 (Fig. 388). Also from loc. 7, colln S3, e.g. BB 72537 (Fig. 389), length 15·6 mm, width 22·1 mm. Also recorded from locs 5 and 6, all in the Alternata Limestone Formation.

Suborder **TRIPLESIIDINA** Moore, 1952
Superfamily **TRIPLECIACEA** Schuchert, 1913
Family **TRIPLECIIDAE** Schuchert, 1913

Genus ***TRIPLESIA*** Hall, 1859

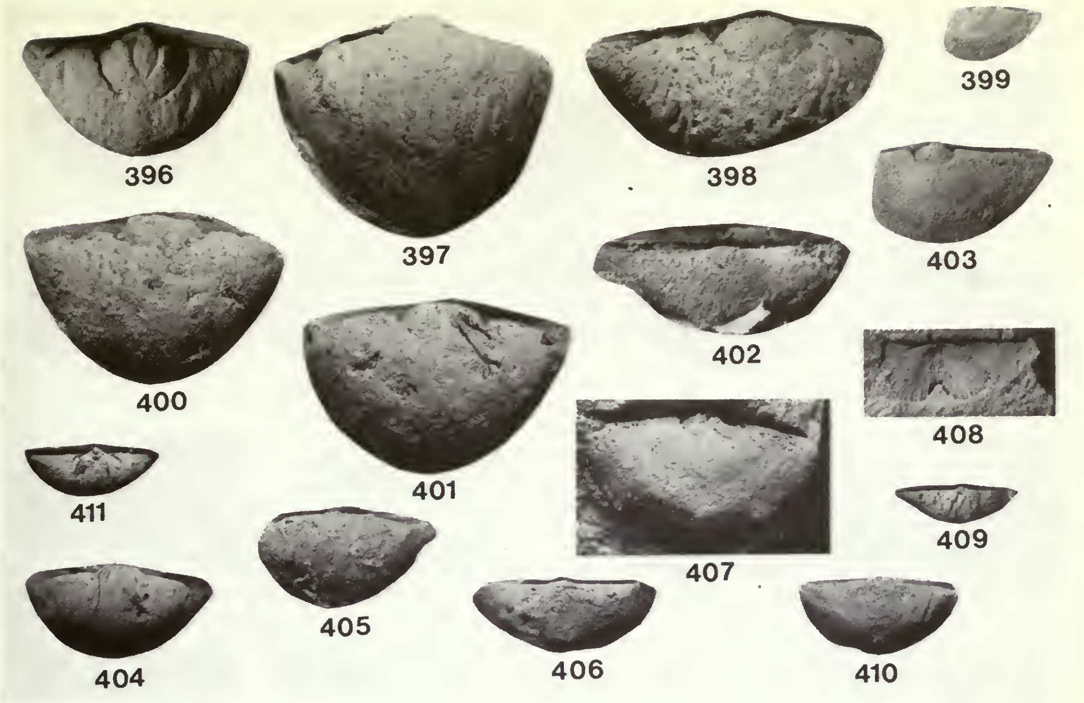
Triplesia sp.
Fig. 350

A distorted internal mould of a pedicle valve (BB 72370) from loc. 44, colln OA13 of the Acton Scott Formation is the sole representative of *Triplesia* in the Upper Caradoc rocks. The valve was approximately 4·5 mm long, 4·8 mm wide and 1·1 mm deep. Its outline was elongately subcircular, with rounded cardinal angles and a deep, slightly angular sulcus. Umbonal area crushed, but the dental lamellae appear short and widely splayed.

Genus ***BICUSPINA*** Havlíček, 1950

Bicuspina sp.
Fig. 351

A distorted internal mould of a pedicle valve (BB 72371) from loc. 43, colln CP4 is the sole representative of *Bicuspina* in the Upper Caradoc. The valve was approximately 6·5 mm long, 10·6 mm wide and 1·7 mm deep. Its outline was subquadrate, with a straight, wide hinge line and with a rounded sulcus. Dental plates thin and divergent; pedicle tube obscured.



Figs 396–411 *Leptestiina oepiki* (Whittington), internal moulds of pedicle valves: 396 = BB 72510, ×2·5, 397 = BB 72510, ×3·0, 398 = BB 72511, ×3, 400 = BB 72509, ×3·2, 401 = BB 72512, ×3·4; external mould of brachial valve: 402 = BB 72513, ×3·2. *Leptestiina* sp., internal moulds of pedicle valves: 399 = BB 72514, ×3, 403 = BB 72515, ×3·7, 407 = BB 72516, ×3; internal mould of brachial valve: 408 = BB 72517, ×3·3. *Eoplectodonta* cf. *rhombica* (M'Coy), internal moulds of pedicle valves: 404 = BB 72519, ×2, 405 = BB 72518, ×1·8, 409 = BB 72521, ×1·5, 410 = BB 72520, ×2, 411 = BB 72519, ×1·4; external mould of brachial valve: 406 = BB 72522, ×1·8.

Order **STROPHOMENIDA** Öpik, 1934
Suborder **STROPHOMENIDINA** Öpik, 1934
Superfamily **PLECTAMBONITACEA** Jones, 1928
Family **LEPTELLINIDAE** Ulrich & Cooper, 1936
Subfamily **LEPTESTIININAE** Havlíček, 1961

Genus *LEPTESTIINA* Havlíček, 1952

Leptestiina oepiki (Whittington)
Figs 396–398, 400–402

1938 *Sampo oepiki* Whittington : 255; pl. 10, figs 15–16; pl. 11, fig. 10.
1963 *Leptestiina oepiki* (Whittington) Williams : 428–430; pl. 10, figs 15, 16, 19–21.
aff.1977 *Leptestiina* aff. *oepiki* (Whittington); Mitchell : 76; pl. 15, figs 1–7.

DESCRIPTION. Elongate, semicircular *Leptestiina* with evenly concavo-convex longitudinal profile, with pedicle valve about 60% as long as wide and 40% as deep as long; ventral interarea apscaline, pseudodeltidium small and apical; ornamentation not known.

Ventral interior with very short blunt teeth, supported by short receding dental plates; ventral muscle field subpentagonal in outline, extending anteriorly for about 30% of the length of the pedicle valve and about 75% as long as wide, adductor field lanceolate, deeply impressed posteriorly and separated from adductor scars by ridges, diductor scars almost meeting anteriorly to surround adductors, whole muscle field surrounded by shell ridges which fuse posteriorly with dental lamellae.

Brachial interior not known.

DIMENSIONS.	length	width
Internal mould of pedicle valve, BB 72509	6·5	10·9
Internal mould of pedicle valve, BB 72510	8·4	12·6
Internal mould of pedicle valve, BB 72511	7·2	13·5
Internal mould of pedicle valve, BB 72512	7·2	10·8
External mould of brachial valve, BB 72513	–	10·7

HORIZON AND LOCALITIES. All figured material from loc. 44, colln OA1. Also recorded from locs 46 and 48.

Leptestiina sp.

Figs 399, 403, 407, 408

DESCRIPTION. Subcircular *Leptestiina* with evenly concavo-convex horizontal profile, with pedicle valve about 60% as long as wide and 35% as deep as long, ventral interarea apscaline, pseudodeltidium small and apical, dorsal interarea short, hypercline; ornament unknown.

Ventral interior with short blunt teeth supported by receding dental lamellae; ventral muscle field pentagonal in outline, extending anteriorly for about 30% of the length of the valve and 75% as long as wide, adductor field lanceolate, weakly impressed, diductor scars almost meeting anteriorly to surround diductor scar.

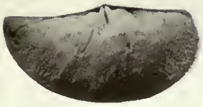
Dorsal interior with simple cardinal process consisting of anteriorly bifurcating, thin shaft connecting with notothyrial platform, socket ridges widely disposed subparallel to hinge defining a pair of oval sockets, lophophore platform 60% as long as wide, weakly defined posteriorly but apparently connecting with distal ends of socket ridges, medially incised anteriorly and ornamented by radiating ridges.

DIMENSIONS.	length	width
Internal mould of pedicle valve, BB 72514	2·4	5·2
Internal mould of pedicle valve, BB 72515	4·0	8·6
Internal mould of pedicle valve, BB 72516	5·7	9·8

HORIZON AND LOCALITIES. All figured material from loc. 47, colln CF1.

DISCUSSION. The few moulds of *Leptestiina* from the Acton Scott Formation show that there are two stocks present, which differ from each other in terms of outline, valve depth and ventral muscle field configuration. However, it is difficult to assess the importance of these differences until more is known about the variability of the stocks.

Figs 412–444 *Sowerbyella sericea* (J. de C. Sowerby), internal moulds of pedicle valves: 412 = BB 73590, ×2, 413 = BB 73591, ×1·8, 414 = BB 73592, ×2, 415 = BB 73593, ×1·9, 416 = BB 73602, ×1·9, 418 = BB 73601, ×1·6, 419 = BB 73604, ×2, 420 = BB 73603, ×2, 421 = BB 73600, ×2; internal moulds of brachial valves: 417 = BB 73607, ×1·8, 423 = BB 73608, ×1·9, 424 = BB 73606a, ×1·8, 426 = BB 73597, ×1·8, 427 = BB 73598, ×2, 428 = BB 73595a, ×1·4, 431 = BB 73609, ×1·8, 432 = BB 73594, ×1·7; external moulds of brachial valves: 422 = BB 73599, ×1·8, 425 = BB 73606b, ×1·9, 429 = BB 73595b, ×1·6, 430 = BB 73596, ×1·6. *Chonetoidea radiatula* (Barrande), internal moulds of pedicle valves: 433 = BB 73568, ×3, 434 = BB 73565, ×3·5, 435 = BB 73566, ×3, 436 = BB 73569, ×3·7, 437 = BB 73567, ×3·6; external moulds of brachial valves: 438 = BB 73576, ×3·6, 439 = BB 73577, ×3·2; internal moulds of brachial valves: 440 = BB 73575, ×2·7, 441 = BB 73573, ×3·8, 442 = BB 73574, ×3, 443 = BB 73572, ×3·2, 444 = BB 73571, ×3·5.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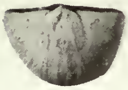
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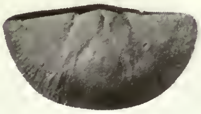
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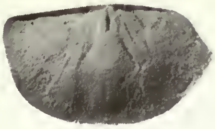
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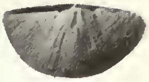
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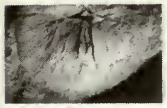
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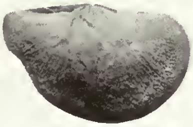
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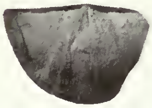
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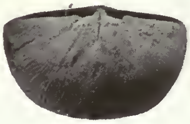
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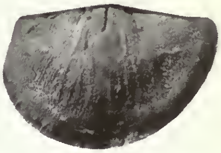
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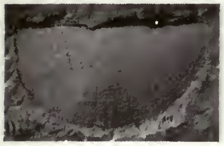
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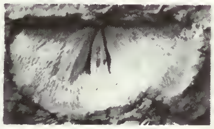
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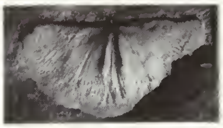
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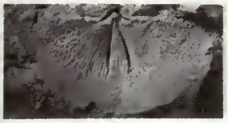
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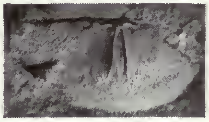
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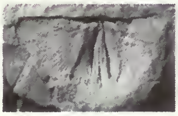
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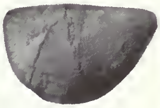
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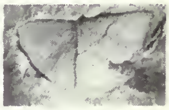
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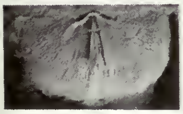
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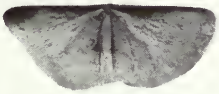
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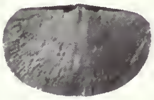
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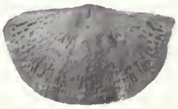
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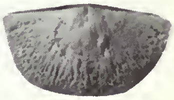
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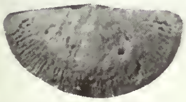
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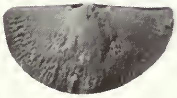
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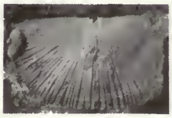
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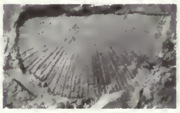
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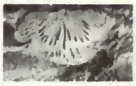
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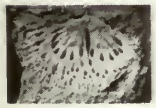
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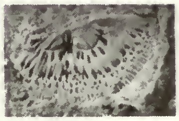
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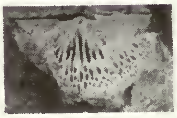
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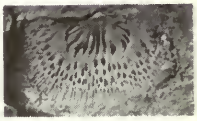
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Family **SOWERBYELLIDAE** Öpik, 1930
Subfamily **SOWERBYELLINAE** Öpik, 1930

Genus ***SOWERBYELLA*** Jones, 1928

Sowerbyella sericea (J. de C. Sowerby)
Figs 412–432

1839 *Leptaena sericea* J. de C. Sowerby *in* Murchison : 636; pl. 19, fig. 1.
1928 *Sowerbyella sericea* (J. de C. Sowerby) Jones : 414; pl. 21, figs 1–4.
1963 *Sowerbyella sericea* (J. de C. Sowerby); Williams : 430–432; pl. 11, figs 1–9.
1970 *Sowerbyella sericea* (J. de C. Sowerby); Bretsky : 85–87; pl. 12, figs 3–6; pl. 13, figs 1–4.
cf. 1974 *Sowerbyella sericea* (J. de C. Sowerby); Williams : 134–135; pl. 24, figs 11–14, 16.

REMARKS. Williams (1963) redescribed and refigured *S. sericea*, based on material from the Alternata Limestone Formation exposed at Soudley Quarry (loc. 7), and it is in no need of revision here. The species is common throughout the Cheney Longville Formation and has been recorded from locs 1 to 33 inclusive, 35, 46 and 47. The specimens figured are derived from the Cheney Longville Formation, selected to give some idea of the variability of this widespread and common stock. Of the figured material BB 73590–1, BB 73594, BB 73595a, b and BB 73596 are from loc. 15, colln W5; BB 73592–3, BB 73597–9 are from loc. 26, colln M15. The remainder come from loc. 25, colln WFT8.

Genus ***EOPLECTODONTA*** Kozłowski, 1929

Eoplectodonta cf. ***rhombica*** (M'Coy)
Figs 404–406, 409–411

1852 *Leptaena sericea* var. *rhombica* M'Coy : 239.
1928 *Sowerbyella rhombica* (M'Coy) Jones : 426–430; pl. 22, fig. 1.
cf. 1963 *Eoplectodonta* cf. *rhombica* (M'Coy) Williams : 448–451; pl. 12, figs 9–14, 18, 19.

DESCRIPTION. Subcircular *Eoplectodonta* with evenly convex longitudinal profile, cardinal angles slightly obtuse, pedicle valve about 50% as long as wide and 30% as deep as long; ventral interarea apscaline, apical pseudodeltidium small; radial ornamentation unknown.

Ventral interior with small elongate teeth, divergent, denticles often developed for over half of hinge line, ventral muscle field strongly impressed, deeply cordate in outline and about 70% as long as wide and extending anteriorly for about 50% of the valve length, small oval adductor scar separated by median ridge, diductor scars widely separated anteriorly.

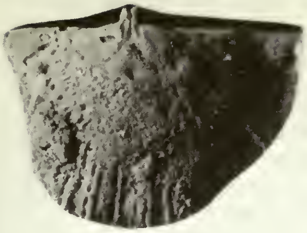
Dorsal valve unknown.

DIMENSIONS.	length	width
Internal mould of pedicle valve, BB 72518	6·7	13·1
Internal mould of pedicle valve, BB 72519	6·4	13·1
Internal mould of pedicle valve, BB 72520	6·8	11·1
Internal mould of pedicle valve, BB 72521	4·3	11·4
External mould of brachial valve, BB 72522	5·7	11·6

HORIZON AND LOCALITIES. All figured material is from loc. 41, colln O104. Also recorded from loc. 40.

DISCUSSION. The few ventral valves of *Eoplectodonta* recovered from the upper Acton Scott Formation of the Onny Valley are best compared with *E.* cf. *rhombica* described by Williams (1963)

Figs 445–456 *Sericoidea homolensis* Havlíček, internal moulds of pedicle valves: 445 = BB 73581, ×9, 446 = BB 73582, ×12·5, 447 = BB 73578, ×11, 448 = BB 73580, ×11, 449 = BB 73579, ×10·7; internal moulds of brachial valves: 450 = BB 73585, ×11·4, 451 = BB 73584, ×13, 452 = BB 73586, ×11·5, 453 = BB 73583, ×10·7, 454 = BB 73587, ×11; external moulds of brachial valves: 455 = BB 73589, ×11·8, 456 = BB 73588, ×11·7.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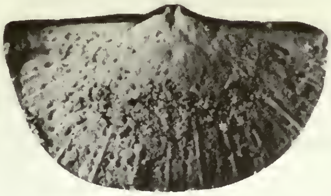
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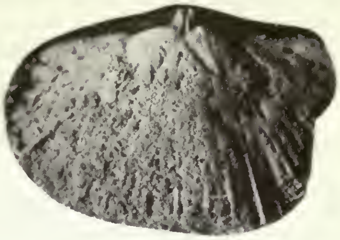
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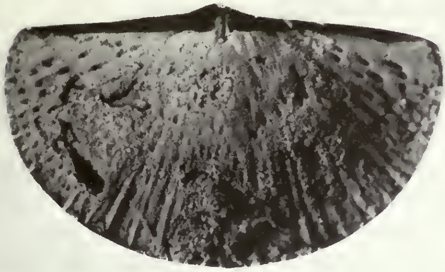
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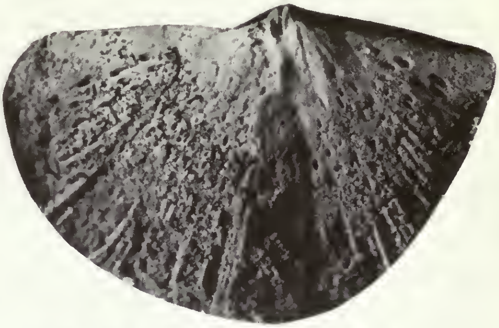
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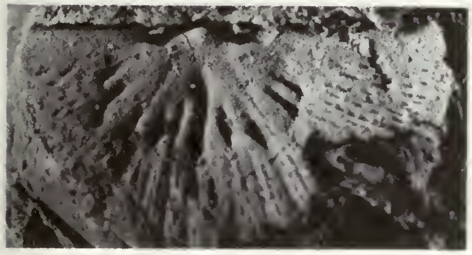
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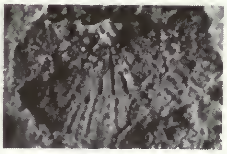
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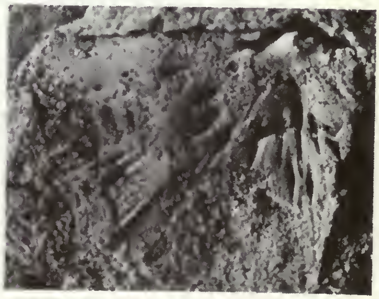
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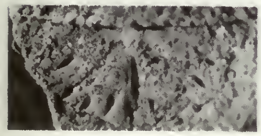
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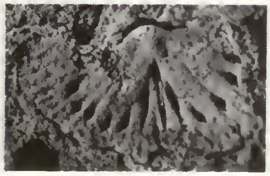
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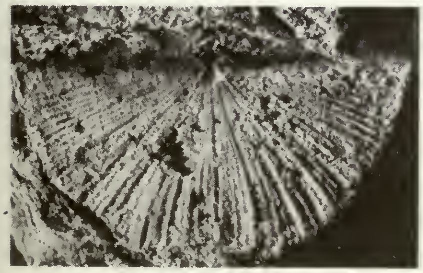
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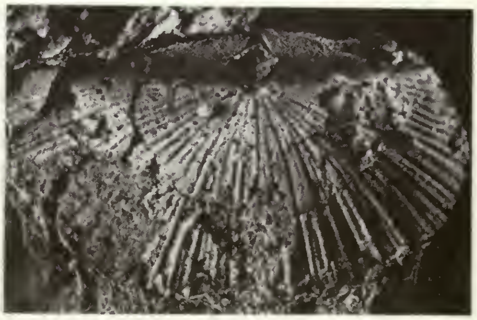
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from the Gelli-grîn Calcareous Ashes (Longvillian) of the Bala district. They are alike in valve and muscle field outline and particularly in the suppression of rugae.

Subfamily **AEGIROMENINAE** Havlíček, 1961

Genus ***CHONETOIDEA*** Jones, 1928

Chonetoidea radiatula (Barrande)

Figs 433–444

1879 *Chonetes radiatulus* Barrande : pl. 54, fig. I, 1–17.
1952 *Chonetoidea radiatula* (Barrande) Havlíček : 405; pl. 3, fig. 8.
1967 *Chonetoidea radiatula* (Barrande); Havlíček : 49; pl. 5, figs. 7–14.
1977 *Chonetoidea radiatula* (Barrande); Mitchell : 93–94; pl. 18, figs 20–36.

Description. Transversely semicircular concavo-convex *Chonetoidea* 60% as long as wide and 15% as deep as long; rectangular cardinal angles with maximum width at hinge, ventral interarea apscaline and possibly with apical pseudodeltidium, dorsal interarea hypercline; ornament finely costellate occasionally with accentuated rib.

Ventral interior with small cordate diductor muscle scar about 30% as long as the valve and 40% as wide as valve length; median oval diductor muscle scar weakly impressed, teeth small, blunt with receding supports, occasional nodes occurring along the hinge line; papillose interior.

Dorsal interior with narrow socket ridges slightly divergent to hinge line and medially ankylosed to ridge-like cardinal process which is produced posteriorly into a trifid head; lophophore platform with strong median septule and up to 7 or 8 strong side septules arranged in an arc at about valve mid-length; adductor muscle field weakly impressed immediately adjacent to inside of median septule.

Dimensions.	length	width
Internal mould of pedicle valve, BB 73565	4·5	6·7
Internal mould of pedicle valve, BB 73566	4·5	7·5
Internal mould of pedicle valve, BB 73567	3·5	7·3
Internal mould of pedicle valve, BB 73568	3·7	6·7
Internal mould of pedicle valve, BB 73569	3·5	6·4
Internal mould of brachial valve, BB 73571	4·0	6·6 (est.)
External mould of brachial valve, BB 73576	3·9	7·3 (est.)
External mould of brachial valve, BB 73577	3·6	6·2

Horizon and localities. All figured specimens are from loc. 46, colln AS6. Also recorded from locs 34–45 inclusive.

Discussion. See p. 281.

Genus ***SERICOIDEA*** Lindström, 1953

Sericoidea homolensis Havlíček

Figs 445–456

1928 *Chonetoidea* ? sp. 2 Jones : 502.
1967 *Sericoidea homolensis* Havlíček : 52–53; pl. 8, figs 1–5.

Description. Transverse semicircular concavo-convex *Sericoidea* 65% as long as wide and 20% as deep as long, maximum width at hinge, ventral interarea apscaline and medially with convex pseudodeltidium, dorsal interarea weakly hypercline to catacline; ornament parvicostellate with bundles of 2 or 3 ribs.

Ventral interior with small, weakly impressed cordate diductor muscle field about 25% as long and 40% as wide as the valve length, adductor scars not known, teeth very short, blunt and divergent, almost parallel with hinge line; finely papillose interior.

Dorsal interior with thin socket ridges subparallel to hinge and united medially with ridge-like cardinal process which has a trifid head; lophophore platform with median septule and up to 5 or 6 often weakly developed lateral septules arranged in an arc at about 65% valve length, adductor scars not known.

DIMENSIONS.	length	width
Internal mould of pedicle valve, BB 73578	2·9	4·3
Internal mould of pedicle valve, BB 73579	4·0	6·0
Internal mould of pedicle valve, BB 73580	3·0	5·5
Internal mould of pedicle valve, BB 73581	3·4	5·0
Internal mould of pedicle valve, BB 73582	2·1	3·7
Internal mould of brachial valve, BB 73585	3·2	5·1
Internal mould of brachial valve, BB 73586	1·9	2·7
External mould of brachial valve, BB 73588	2·5	5·3
External mould of brachial valve, BB 73589	2·7	4·5

HORIZON AND LOCALITIES. All figured specimens are from the Onny Shale Formation, loc. 50, colln O36. Also recorded from locs 49 and 51.

DISCUSSION. According to Mitchell (1977 : 93) the distinction between *Chonetoidea* and *Sericoidea* is based primarily on the former having fine canals penetrating the ventral interarea, usually preserved as small nodes (see Cocks 1970) and finely costellate as opposed to parvicostellate ribbing. The presence of nodes has only been noted with certainty in *C. radiatula*; an occasional specimen of *S. homolensis* may have them, however, although the evidence is equivocal owing to the poor preservation. Ribbing patterns are also variable and it is not impossible, given larger and better-preserved collections, that all gradations between the two may be found in one population. Certainly there seems to be a stratigraphical trend from *Chonetoidea* to *Sericoidea* type ribbing patterns predominating in a population, but again owing to the lack of well-preserved material (and lack of outcrop) it is not known if the gradation is disjunct or continuous. Although the two genera are here kept separate pending a comprehensive taxonomic treatment based on large populations traced through continuous sections, it is felt that *Sericoidea* may prove to be a synonym of *Chonetoidea*.

C. radiatula from the type Caradoc agrees in all morphological details with topotype material (Havlíček 1967). In terms of septule arrangement it closely resembles *C. stoermeri* from the Ordovician of the Oslo region (Spjeldnaes 1957).

S. homolensis appears to be the *Sericoidea* with the most complex septule arrangement; cf. *S. restricta* (Lindström 1953) and *S. abdita* (Whittington & Williams 1955). The Caradoc specimens agree with the Bohemian species *S. homolensis* in all aspects of morphology.

Jones (1928) had at his disposal the internal mould and cast of a single pedicle valve from the Onny Shale collection of Reynolds. He doubtfully assigned this to *Chonetoidea*, but although he did not figure it, it probably belongs to *S. homolensis* on stratigraphical grounds.

Superfamily **STROPHOMENACEA** King, 1846
Family **STROPHOMENIDAE** King, 1846
Subfamily **STROPHOMENINAE** King, 1846

Genus ***STROPHOMENA*** de Blainville, 1825

Strophomena grandis (J. de C. Sowerby)
Figs 457–466

1839 *Orthis grandis* J. de C. Sowerby *in* Murchison : 638; pl. 20, figs 12, 13.
1933 *Longvillia grandis* (J. de C. Sowerby) Bancroft : 3.
1963 *Strophomena grandis* (J. de C. Sowerby) Williams : 452–453; pl. 12, figs 17, 20, 21; pl. 13, fig. 2.

DISCUSSION. Williams (1963) redescribed and refigured *S. grandis* but in doing so he redefined the species based on moulds from the *Dalmanella wattsi* beds (Bancroft 1945) of Marshwood Quarry (loc. 27). My extensive collections indicate that *S. grandis* is very rare at this horizon, being far more abundant in the overlying *D. unguis* beds. However, at Marshwood Quarry almost all the exposure of the *D. wattsi* beds is represented by what Bancroft (1929*a*) referred to as the *Heterorthina praecuIta* beds, which are now included in the *D. wattsi* beds, and represent a faunal and sedimentary facies transition between the *D. wattsi* and *D. unguis* beds.

Within the topmost strata of the *D. wattsi* beds (= *H. praeculta* beds) *S. grandis* occurs sparingly, and it is from this horizon that Williams probably obtained his *S. grandis* material which is morphologically indistinguishable from *S. grandis* in the overlying *D. unguis* beds. However, below the *H. praeculta* horizon of the *D. wattsi* beds very rare *Strophomena* occur which for the present are referred to *S. grandis* until more is known about the variability of the stock. The few specimens available for study appear to differ from typical *S. grandis* in being more transverse, finer-ribbed (5 or 6 costellae per mm, 10 mm anteromedially of the dorsal umbo) and in having a less impressed ventral muscle field.

DIMENSIONS.	length	width
Internal mould of brachial valve, BB 73533	30·1	46·8
Internal mould of brachial valve, BB 73534	34·5	42·3
Internal mould of brachial valve, BB 73535	25·2	–
Internal mould of pedicle valve, BB 73537	28·2	40·8
Internal mould of pedicle valve, BB 73538	26·2	36·8
Internal mould of pedicle valve, BB 73539	26·1	38·0
Internal mould of pedicle valve, BB 73540	23·3	39·9

HORIZON AND LOCALITIES. BB 72533–8 inclusive are from loc. 24, colln WFT1 of the *D. unguis* beds. BB 73539 (loc. 27, colln M1), BB 73540 (loc. 19, colln CL2), BB 72541–2 (loc. 32, collns LM4 and LM1 respectively) are from the *D. wattsi* beds of Bancroft (1933). Also recorded from locs 21, 23, 26 and 28–33.

Subfamily **RAFINESQUININAE** Schuchert, 1893

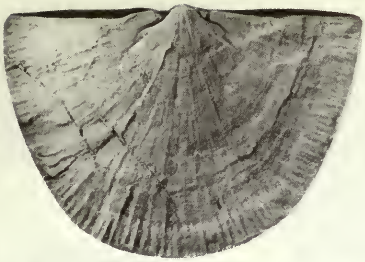
Genus ***KJAERINA*** Bancroft, 1929

DIAGNOSIS (emended). Elongately triangular to semicircular alate strophomenides, with weakly to moderately strongly convex, dorsally geniculate pedicle valve and plane to anteriorly weakly dorsally geniculate brachial valve, skirt short and rounded, gently angulate, geniculate specimens with semicircular disc; ornamented by unequal parvicostellae and with very prominent medial rib, and posterolaterally along hinge with very fine irregular rugae; ventral interarea apscaline with vestigial pseudodeltidium; dorsal interarea anacline medially with small convex grooved chilidium; finely pseudopunctate.

Ventral interior with short, squat, obliquely-placed teeth bisecting angle between hinge and receding dental plates which support them; dental plates narrowly divergent, extending anteriorly as low ridges laterally bounding ventral muscle field, ventral muscle scar narrow, triangular medially, with a lanceolate adductor scar on a shallow platform which is sometimes completely surrounded by diductor tracks.

Dorsal interior with delicate cardinalia consisting of a small splayed cardinal process posteriorly ankylosed to narrowly divergent socket ridges, notothyrial platform often strongly developed, anchor-shaped, bounding oval hollows of posterior adductors, rounded shallow medial ridge separating adductors.

Figs 457–476 *Strophomena grandis* (J. de C. Sowerby), internal moulds of pedicle valves: 457 = BB 73537, ×1·2, 458 = BB 73539, ×0·9, 459 = BB 73540, ×0·9, 461 = BB 73541, ×0·8, 462 = BB 73538, ×0·8, 463 = BB 73536, ×0·8; internal moulds of brachial valves: 460 = BB 73535, ×1·2, 464 = BB 73542, ×1·1, 465 = BB 73533, ×1·2, 466 = BB 73534, ×1·1. *Kjaerina bipartita* (Salter), internal moulds of pedicle valves: 467 = BB 73558, ×1·2, 468 = BB 73557, ×0·9, 469 = BB 73556, ×1·3, 470 = BB 73554, ×1·1, 471 = BB 73555, ×1·1, 472 = BB 73559a, ×1·5; internal moulds of brachial valves: 474 = BB 73562, ×1·5, 475 = BB 73561, ×1·2, 476 = BB 73560, ×1·3; external mould of pedicle valve: 473 = BB 73559b, ×1·3.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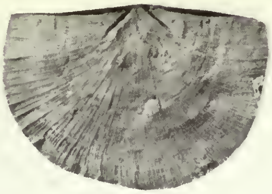
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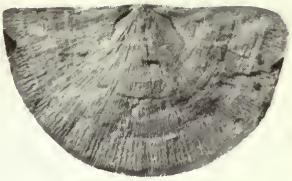
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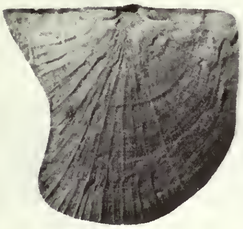
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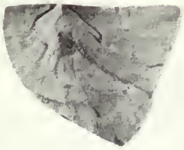
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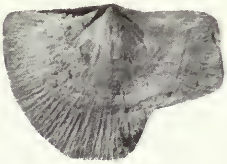
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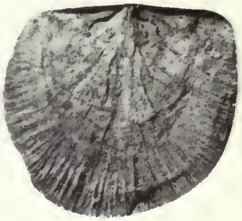
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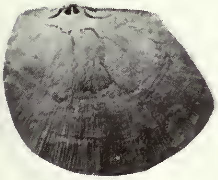
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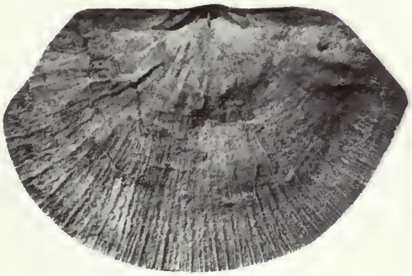
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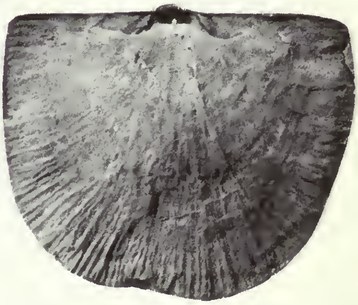
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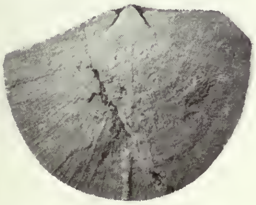
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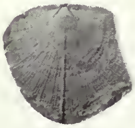
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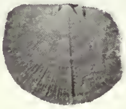
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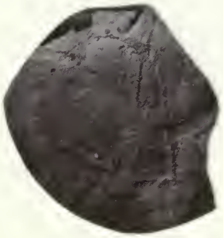
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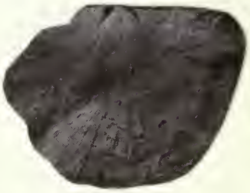
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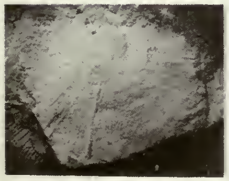
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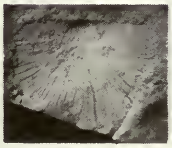
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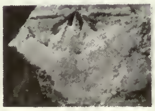
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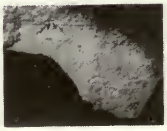
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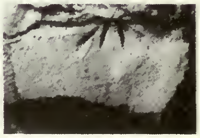
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TYPE SPECIES. *Kjaerina typa* Bancroft, 1929, by original definition of Bancroft (1929*a* : 43).

DISCUSSION. The chequered taxonomic history of *Kjaerina* is closely related to that of *Hedstroemina* and is discussed under the latter genus, p. 287.

Kjaerina bipartita (Salter)
Figs 467–473

1854 *Strophomena bipartita* Salter : 74.
1929*a* *Kjaerina bipartita* (Salter) Bancroft : 52–53; pl. 1, fig. 14.
1945 *Kjaerina bipartita* (Salter); Bancroft : 248–249; pl. 37, figs 3–4.
1958 *Kjaerina bipartita* (Salter); Dean : pl. 24, fig. 19.
1978 *Kjaerina bipartita* (Salter); Cocks : 112.

DESCRIPTION. Semicircular, gently plano-convex *Kjaerina*, with a pedicle valve about 80% as long as wide and evenly convex, brachial valve plane with rectangular cardinal angles, ventral interarea apscaline, pseudodeltidium vestigial, dorsal interarea anacline, chilidium small, arched and only covering dorsal end of cardinal process lobes, radial ornamentation unequally parvicostellate with commonly 4 costellae per mm, 10 mm anteromedially of ventral umbo, and always with strongly accentuated median rib.

Ventral interior with very small teeth oblique to hinge line and fused to short receding dental lamellae which extend forward for 15% of the valve length, ventral muscle field rounded triangular, faintly impressed, as wide as long and 25% as long as the valve with submedian lanceolate adductor scar occasionally surrounded by diductor tracks.

Dorsal interior with short delicate cardinal process lobes ankylosed to narrowly divergent socket ridges which extend forward for about 10% of the valve length, notothyrial platform and median ridge faintly developed, posterior adductor scars faintly impressed.

DIMENSIONS.	length	width
Internal mould of pedicle valve, BB 73555	22·4 (est.)	30·4 (est.)
Internal mould of pedicle valve, BB 73556	10·2	14·2 (est.)
Internal mould of pedicle valve, BB 73557	13·5 (est.)	14·3 (est.)
Internal mould of pedicle valve, BB 73558	22·0	27·4
Internal and external mould of pedicle valve, BB 73559a, b	12·3	14·7

HORIZON AND LOCALITIES. BB 73554–5 and BB 73562 from loc. 17, colln S9; BB 73556–8 and BB 73561 from loc. 17, colln S7; BB 73559a, b and BB 73560 from loc. 1, colln CL9. Also recorded from locs 2–8, 13, 14 and 16.

DISCUSSION. See p. 286.

Kjaerina typa Bancroft
Figs 477–498

1929*a* *Kjaerina typa* Bancroft : 53–54; pl. 1, fig. 15.
1929*a* *Kjaerina geniculata* Bancroft : 54–55; pl. 1, figs 16–17.
1945 *Kjaerina geniculata* Bancroft; Bancroft : 249–256; pl. 37, figs 5–7.
1958 *Kjaerina typa* Bancroft; Dean : pl. 24, fig. 20.

DESCRIPTION. Elongately semicircular to triangular, gently plano-convex to concavo-convex,

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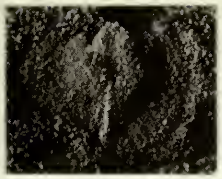
Figs 477–498 *Kjaerina typa* Bancroft, internal moulds of pedicle valves: 477 = BB 73626, ×11·5, 478 = BB 73627, ×9·5, 479 = lectotype BB 14383, ×1·5, 480 = BB 73637, ×0·8, 481 = BB 73628, ×3·1, 482 = BB 73630, ×0·8, 483 = BB 73631, ×1, 484 = BB 73632, ×0·8, 485 = BB 73636, ×0·8, 486 = BB 73633, ×0·9, 487 = BB 73639, ×1, 488 = BB 73635, ×0·9, 489 = BB 73629, ×1·4, 490 = BB 73634, ×1·2, 491 = BB 73640, ×1·2, 492 = BB 73638, ×1·2; internal moulds of brachial valves: 493 = BB 73645, ×1·1, 494 = BB 73644, ×1·1, 495 = BB 73641, ×10·8, 496 = BB 73646, ×1·9, 497 = BB 73642, ×1·7, 498 = BB 73643, ×4.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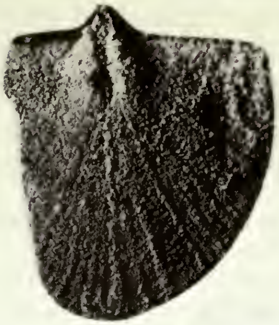
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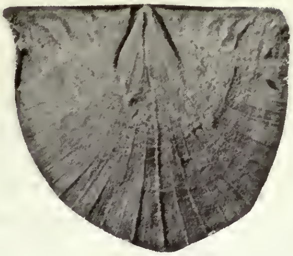
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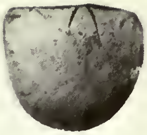
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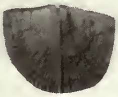
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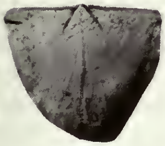
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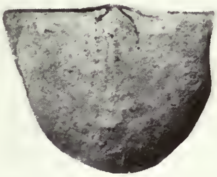
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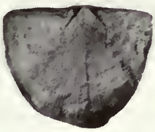
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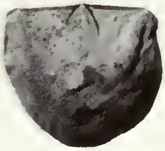
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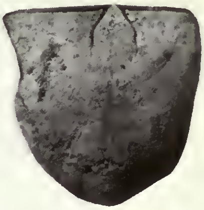
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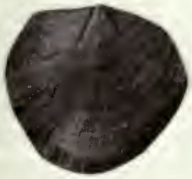
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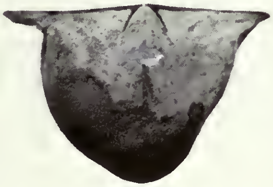
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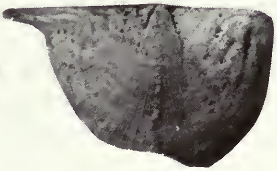
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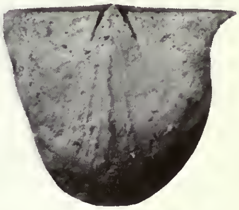
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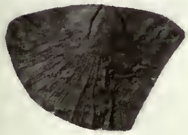
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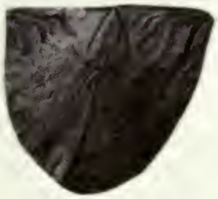
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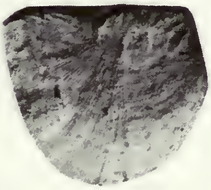
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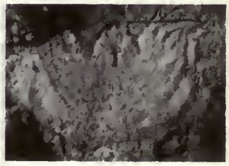
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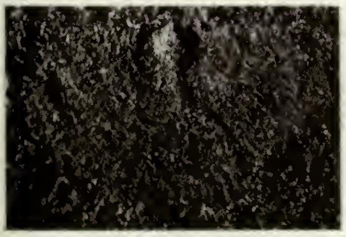
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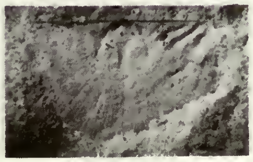
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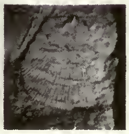
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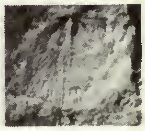
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weakly to strongly dorsally geniculate alate *Kjaerina*, with a pedicle valve about 75% as long as wide, initially weak to moderately convex becoming plane anteriorly; valve gently geniculate, trail approximately up to 30% as long as valve length; disc if present oval and covered with posterolateral impersistent, weak rugae; ventral interarea apscaline, pseudodeltidium appearing absent, dorsal interarea anacline with small arched chilidium; radial ornamentation unequal parvicostellate, commonly with 4 ribs per mm, 10 mm anteromedially of the ventral umbo.

Ventral interior with small stubby teeth acute to hinge line and supported by narrowly divergent receding dental lamellae extending forward for about 10% of the valve length; muscle field as broad as long and extending forward for 50% of the valve length and bounded laterally by shell ridges extending from dental plates, submedian adductor scar raised on small platform and occasionally with transmuscle septa; diductor tracks may completely surround adductor tracks.

Dorsal interior with small, delicate, bilobed cardinal process posteriorly ankylosed to weakly divergent socket ridges which extend anteriorly for approximately 20% of the valve length, notothyrial platform weakly to strongly developed, anchor-shaped, shallow median ridge separating small posterior adductor muscle impressions.

ONTOGENY. Collection O110 from loc. 12, the type locality for *K. typa*, afforded numerous small individuals of both valves allowing an ontogenetic series for the species to be established. The pedicle valves of small individuals (c. 2 mm wide) are characterized by a massive bulbous convex protegular node with relatively thick teeth and dental plates fused to it posteriorly. There is already differentiation of the diductor and adductor tracks, and the strong median rib so characteristic of *Kjaerina* is already established (Fig. 477), and penetrates into the node. With growth the node is consumed in the ventral muscle field and assumes a more triangular shape. The teeth and dental plates decrease relatively in size and by 4 or 5 mm in size (width) individuals have attained adult characteristics (Fig. 481). With brachial valves, initially (valve width c. 2·5 mm wide) the protegular node is a convex Y shape with the median ridge and socket plates fused to it anteriorly and laterally, whilst posteriorly a small bilobed cardinal process is also attached to it. With growth the node differentiates and by 4 mm valve width the adult characters are present.

MATERIAL AND LOCALITIES. Lectotype (Fig. 479) BB 14383 (selected Cocks 1978 : 113), est. length 22·3 mm, est. width 25·2 mm, from loc. 12. Also from loc. 12 (colln O110) BB 73626 (Fig. 477), length 1·8 mm, width 2·0 mm; BB 73627 (Fig. 478), length 3·4 mm, width 4·8 mm; BB 73628 (Fig. 481), length 3·7 mm, width 5·0 mm; BB 73641 (Fig. 495); BB 73643 (Fig. 498); BB 73642 (Fig. 497), and from colln O22 BB 73638 (Fig. 492), length 19·9 mm, est. width 22·7 mm, and colln O113 BB 73639 (Fig. 487), length 22·4 mm and BB 73640 (Fig. 491). Also from loc. 9, with more than 24 individuals on one slab, including BB 73629–37 (Figs 480, 482–6, 488–90) and BB 73644–6 (Figs 493–4, 496), and locs 10, 11, 15 and 18, all from the Glynboro Member of the Cheney Longville Formation.

DISCUSSION. Bancroft (1929*a*) proposed ten new species in his genus *Kjaerina*. Two of these, *K. typa* and *K. geniculata*, as well as *K. bipartita* (Salter), occur in the upper Caradoc.

The type locality for *K. bipartita* is ambiguous. Salter (1854) reported the shells to be found near Hope Bowdler, Cheney Longville and in thin flags of the Horderley section. Bancroft (1929*a* : 52) assumed that this meant that the species was based on material from the middle part of the Alternata Limestone of Cheney Longville. Thus, in his erection of *Kjaerina* species, *K. bipartita* is based on material from this horizon. From the description of Salter in finding *K. bipartita* in thin flags (which presumably indicates the presence of parallel laminae), the material is most likely to derive from the Alternata Limestone or lower Cheney Longville Formation.

Based on material from the Alternata Limestone Formation and lowest Cheney Longville Formation of the Caradoc district (note that Salter indicated the species to occur throughout the district), *K. bipartita* differs from other upper Caradoc *Kjaerina* in its weakly plano-convex shell, lack of posterolateral rugae, faintly impressed ventral muscle areas, small teeth and receding dental plates and semicircular outline.

K. geniculata is very rare at the type locality (loc. 10 of this report) but a large topotype population of *K. typa* was obtained (loc. 12 of this report) and the morphological variation expressed by this population encompasses *K. geniculata* in every respect. Perhaps the most striking difference between the two species, according to Bancroft's descriptions, was the dorsal geniculation of *K. geniculata*. However, this is a continuously variable character and end members of *K. typa* variation series are also geniculate. Contrary to the assertions of Bancroft, geniculation also affects brachial valves (Figs 493–8). It should also be noted that Bancroft (1929*a* : 54) admitted that 'it is thus a matter of considerable embarrassment to know where to draw the line between different species'. Here he was talking about the difficulties of separating *K. typa* from *K. geniculata*, though in all fairness it should be stated that he was more concerned with the stratigraphical subdivision.

In view of the close morphological similarity between the two species, *K. geniculata* is here synonymized with *K. typa*.

Genus ***HEDSTROEMINA*** Bancroft, 1929

DIAGNOSIS (emended). Weakly to strongly plano-convex to concavo-convex strophomenides, weakly to strongly dorsally geniculate with a weak anterior sulcus, skirt short to long and rounded to abruptly angulate with semirounded disc; ornamented by unequal parvicostellate ribs and often with prominent medial rib and very impersistent concentric wrinkles; ventral interarea apscaline with small to large apical foramen and vestigial or resorbed pseudodeltidium, dorsal interarea anacline to orthocline with convex, medially groved chilidium; finely pseudopunctate.

Ventral interior with short, squat, obliquely-placed teeth, supported by short to long, thin to thick, narrowly to widely divergent dental plates which may extend forward to bound the muscle field laterally, ventral muscle scar wide, triangular to subcircular, often flabellate and posteriorly consisting of a submedian lanceolate adductor scar, sometimes on a platform of transmuscle septa and completely surrounded by diductor scars, lanceolate ventral adjustor scars parallel to dental plates.

Dorsal interior with delicate cardinalia consisting of a slightly splayed bilobed blade-like cardinal process ankylosed posteriorly to thin divergent socket ridges and anteriorly to slightly raised broad median ridge, notothyrial platform weakly to moderately developed as a raised anchor-shaped feature bounding shallow oval hollows corresponding to the attachment sites of the posterior adductors.

TYPE SPECIES. *Hedstroemina fragilis* Bancroft, 1929, by original designation of Bancroft (1929*a* : 56).

DISCUSSION. Bancroft erected *Hedstroemina* for a group of Marshbrookian and post-Marshbrookian concavo-convex, subgeniculate or dorsally geniculate rafinesquinids. In doing so he recognized the close similarity between *Hedstroemina* and *Kjaerina bipartita*, but stated that they could be distinguished by the geniculate or sharply flexed dorsal valve and the regular type of ribbing in *Hedstroemina*. However, the geniculation and deflection of the dorsal valve in *Hedstroemina* are highly variable features and specimens often resemble the geniculate *K. typa*. Further, the ribbing type of *Hedstroemina* is very similar to *Kjaerina*.

Salmon (1942 : 570–571) synonymized *Kjaerina* and *Hedstroemina* with *Rafinesquina*, believing them to be essentially the same stock. Spjeldnaes (1957 : 129–130) reported that the differences between the genera are concerned mainly with ventral musculature, geniculation and ribbing. He listed *Kjaerina* as having narrowly divergent ventral muscle impressions, a non-geniculate or only slightly geniculate ventral valve and always a flat dorsal valve. In contrast, *Hedstroemina* supposedly had widely divergent ventral muscle impressions and strongly dorsally geniculate valves. The extreme variability of such features led Spjeldnaes to regard the two genera simply as subgenera of *Rafinesquina*.

Williams *et al.* (1965) kept *Kjaerina* and *Rafinesquina* as separate genera, distinguishing between the two on the much stronger posterolateral rugae development of *Kjaerina* and also the low subparallel bounding ridges around a lightly impressed ventral muscle field. *Hedstroemina* was placed as a subgenus of *Kjaerina*, distinguished from it by its commonly strongly dorsally geniculate valves and rarity of thickened median costae.

Rafinesquina, *Kjaerina* and *Hedstroemina* are clearly all very close morphologically. However, the characters used by Williams *et al.* (1965) to distinguish between the *Kjaerina* group and *Rafinesquina* are applicable, since the two taxa can be consistently recognized by them. In this study *Hedstroemina* is consistently distinguished from *Kjaerina* by the following characteristics:

1. The convex and commonly strongly dorsally geniculate pedicle valve, and concave or weakly geniculate brachial valve
2. The wider, more impressed ventral musculature plus the common occurrence of trans-muscle septa
3. The more heavily calcified bilobed cardinal process
4. The less strongly developed median costae and the crinkly appearance (weak rugae ?) of the shell surface
5. Thinner socket ridges.

Hedstroemina fragilis Bancroft
Figs 499–515

1929*a* *Hedstroemina parva* Bancroft : 57–58; pl. 2, figs 4–5.
1929*a* *Hedstroemina fragilis* Bancroft : 58–59; pl. 2, figs 1–3.
1929*a* *Hedstroemina robusta* Bancroft : 59; pl. 2, figs 6–7.
cf. 1957 *Rafinesquina* (*Hedstroemina*) cf. *robusta* (Bancroft) Spjeldnaes : 133–134; pl. 8, fig. 5.
aff. 1957 *Rafinesquina* (*Hedstroemina*) aff. *robusta* (Bancroft) Spjeldnaes : 134–135; pl. 8, figs 1–4.

DESCRIPTION. Plano-convex to concavo-convex dorsally weakly to strongly geniculate *Hedstroemina*, semicircular in outline, 75% as long as wide, disc if present semicircular; shell surface covered by concentric wrinkles, ventral interarea apscaline and with small to large apical foramen and vestigial pseudodeltidium, dorsal interarea anacline to orthocline with convex, medially grooved chilidium; radial ornamentation unequally parvicostellate, commonly with 5 ribs per mm, 10 mm anteromedially of the umbones.

Ventral interior with short stubby teeth placed to bisect angle between hinge and receding dental plates which support them and extend forward for about 18% of the valve length; ventral muscle field rounded triangular, somewhat flabellate and surrounded laterally by fine shell ridges, often as wide as long and extending forward for about 35% of the valve length, muscle field of larger specimens often traversed longitudinally by fine shell ridges.

Dorsal interior with blade-like, bilobed, splayed cardinal process ankylosed posteriorly to socket ridges which extend forward for about 20% of the valve length, anchor-shaped notothyrial platform well-developed in larger individuals, median ridge low and separating slightly etched posterior adductor scars.

MATERIAL AND LOCALITIES. Lectotype (Fig. 499) BB 14380 (selected Cocks 1978 : 112), length 22·0 mm, est. width 26·6 mm, from loc. 25, as is BB 73879 (Fig. 506), Bancroft colln, length 26·3 mm, width 27·0 mm, and (colln WFT7) BB 73545 (Fig. 502), length 10·5 mm, est. width 17·0 mm. Also from loc. 28, colln M12, e.g. BB 73551 (Fig. 512), BB 73552 (Fig. 514), BB 73553 (Fig. 505); loc. 43, colln CP2, e.g. BB 73543 (Fig. 507), BB 73544 (Fig. 503), and loc. 45, colln AS1,

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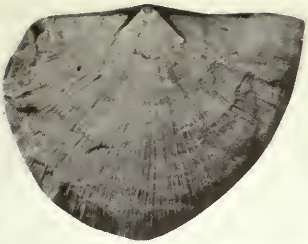
Figs 499–523 *Hedstroemina fragilis* Bancroft, internal moulds of pedicle valves: 499 = lectotype BB 14380, ×1·5, 500 = lectotype of synonymized *H. robusta* BB 14384, ×1·5, 501 = lectotype of synonymized *H. parva*, BB 14385, ×1·5, 502 = BB 73545, ×1·4, 503 = BB 73544, ×1·1, 504 = BB 73546, ×1·1, 505 = BB 73553, ×0·8, 506 = BB 73879, ×1·2, 507 = BB 73543, ×0·8, 509 = BB 73547a, ×1·3, 510 = BB 73548a, ×1·4; internal moulds of brachial valves: 512 = BB 73551, ×1·4, 513 = BB 73932, ×1, 514 = BB 73552, ×1; external moulds of pedicle valves: 508 = BB 73547b, ×1·6, 511 = BB 73548b, ×1·3; external mould of brachial valve: 515 = BB 73550, ×1·4. ? *Zygospira* sp., internal moulds of brachial valves: 516 = BB 72528, ×4, 517 = BB 72525, ×3·7, 520 = BB 72524, ×4, 521 = BB 72526, ×4; internal moulds of pedicle valves: 518 = BB 72527, ×3·2, 519 = BB 72523, ×3·7. *Kjerulfina polycyma* Bancroft, internal mould of brachial valve: 523 = BB 73901, ×1·1; external mould of brachial valve: 522 = BB 73897, ×1·7.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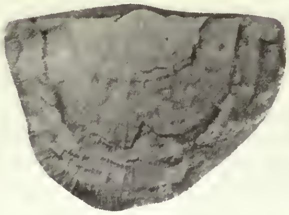
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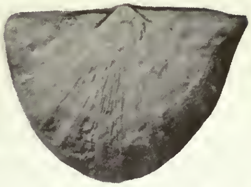
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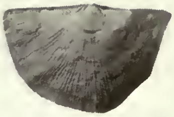
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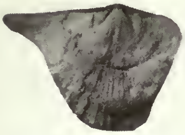
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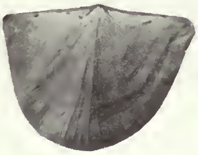
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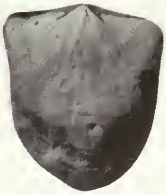
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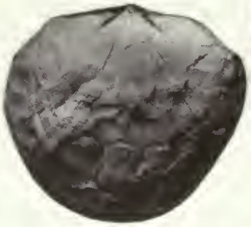
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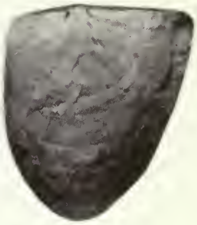
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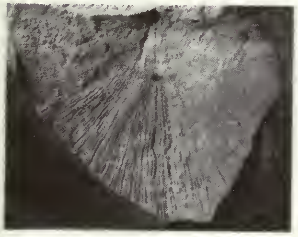
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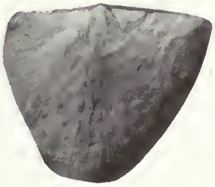
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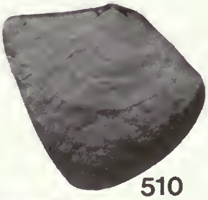
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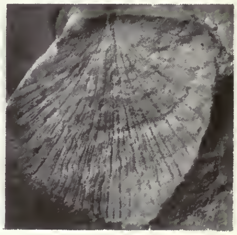
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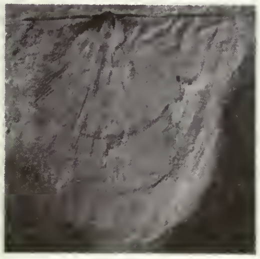
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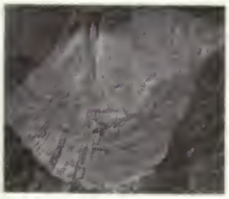
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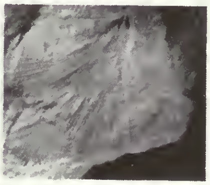
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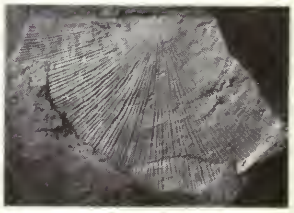
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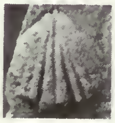
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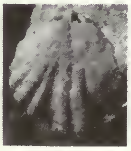
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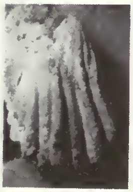
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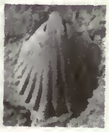
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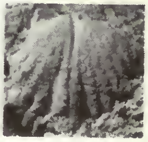
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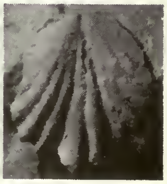

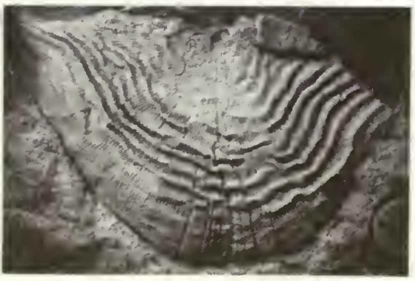
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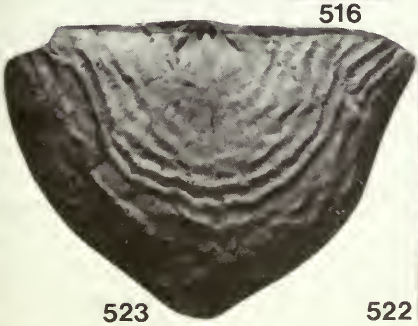
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e.g. BB 73549–50 (Fig. 515). Loc. 47, Dean colln, e.g. BB 73546 (Fig. 504), BB 73547 (Figs 508–9), BB 73548 (Figs 510–1). Also from Dean colln, the old quarry, quarry field, Gretton, e.g. BB 73932 (Fig. 513). BB 14385 (Fig. 501) is lectotype of *parva* and is from Upper Barn, Wistanstow. Also known from locs 22, 27, 34–42, 44, 46 and 47, all in the upper Cheney Longville Formation and Acton Scott Formation.

Discussion. Bancroft (1929*a*) erected three species of *Hedstroemina*, *H. parva*, *H. fragilis* and *H. robusta*. His descriptions were based only on ventral valves for *H. parva*, 'invariably much buckled and fractured' specimens of *H. fragilis*, and for *H. robusta* he concluded 'the material for this species is very poor' (Bancroft 1929*a* : 57–59).

H. fragilis is by far the most common species, a fact noted by Bancroft. Analysis of the variation expressed by the topotype population indicates a wide range, but one in which all the morphological characters are linked by a continuous morphological gradient. For instance, almost plane shells are linked continuously to strongly convex geniculated types. The variation expressed by this topotype population of *H. fragilis* completely encompasses the other two species; *H. parva* and *H. robusta* are therefore synonymized with *H. fragilis*.

Genus ***KJERULFINA*** Bancroft, 1929

Diagnosis (emended). Weakly concavo-convex, ventrally geniculate, anteriorly weakly sulcate semicircular strophomenides with a triangular disc; ornamented by unequal parvicostellae and fine concentric growth lines, disc ornamented by fine to coarse irregular rugae; ventral interarea apscaline with small supra-apical foramen and resorbed pseudodeltidium, dorsal interarea apscaline with very small convex chilidium; finely pseudopunctate.

Ventral interior with short, stubby, obliquely placed teeth supported by short, thin, receding dental plates, ventral muscle scar flabellate, elongately subquadrate in outline and consisting of a submedian lanceolate adductor scar bounded by fine ridges and completely surrounded by diductor scars, lanceolate ventral adjustor muscles parallel to the dental plates, whole muscle complex bounded by fine muscle ridges.

Dorsal interior with fairly delicate cardinalia consisting of a slightly splayed bilobed cardinal process posteriorly ankylosed to slightly divergent thin socket ridges; notothyrial platform poorly developed as a slightly raised feature bounding oval hollows corresponding to the attachment site of the posterior adductors, median ridge low and broad.

Type species. *Kjerulfina trigonalis* Bancroft, 1929, by original definition of Bancroft (1929*a* : 59).

Discussion. Bancroft (1929*a* : 59) erected this genus to embrace shells with valves of leptaenoid shape, trigonal or subparabolic contour and with an abruptly geniculate ventrally deflected border. Certainly the abrupt ventral deflection is probably the most characteristic feature of the shell. Bancroft was perplexed by this character, which he thought detracted from placing the genus in a group with *Rafinesquina* (1929*a* : 60). He suggested that it might belong to the Orthotetinae of Waagen, an assignment he later confirmed (1945 : 250). Spjeldnaes (1957) placed *Kjerulfina* in the subfamily Strophomeninae King, 1946, along with *Rafinesquina*. He also expanded the generic diagnosis of *Kjerulfina* to include amongst other things forms lacking a ventrally deflected geniculation. He consequently experienced difficulty in distinguishing *Kjerulfina* from *Strophomena* and *Holtedahlina*, and the criteria he used, e.g. outline of the ventral muscle field and attitude of the intermuscle ridges, are untenable.

Kjerulfina was placed in the subfamily Rafinesquininae Schuchert, 1893 by Williams *et al.* (1965), an assignment which is owing to its close similarity to *Rafinesquina* in all aspects except geniculation.

Kjerulfina trigonalis Bancroft
Figs 524–535, 538

1929*a* *Kjerulfina trigonalis* Bancroft : 61; pl. 2, figs 8–9.

Description. Gently concavo-convex ventrally geniculate *Kjerulfina*, semielliptical to semicircular in outline and 70% as long as wide, larger individuals alate, pedicle valve initially convex, 10% as deep as shell width becoming plane anteriorly; valve abruptly geniculate, trail about 15% as long as shell width, disc rounded triangular in outline and surface covered with very irregular weak rugae; ventral interarea apscaline and with small supra-apical foramen, pseudodeltidium appears absent, dorsal interarea apscaline with small arched chilidium; radial ornamentation unequally parvicostellate, often with the median rib thickened and with usually 4 ribs per mm, 10 mm anterior of the dorsal umbo.

Ventral interior with short teeth parallel to the weakly divergent receding dental plates which extend forward for 5% of the valve length; ventral muscle field elongately subquadrate and flabellate, surrounded by fine ridges extending anteriorly from dental plates, 66% as wide as long and extending forward for 40% of the length of the valve, fine ridges defining a median lanceolate adductor scar which is surrounded anteriorly by the adductor scars.

Dorsal interior with delicate elliptical bilobed cardinal process which is slightly splayed and ankylosed posteriorly to divergent thin socket ridges reaching anteriorly for 14% of the length of the brachial valve, notothyrial platform weakly developed, anchor-shaped, median ridge low and broad.

MATERIAL AND LOCALITIES. Lectotype (Fig. 524) BB 73834 (selected Cocks 1978 : 110), est. length 23·3 mm, est. width 38·0 mm, from loc. 27, also (colln M4) BB 72542 (Fig. 532), length 21·0 mm, width 26·6 mm. Also loc. 24, colln WFT1, e.g. BB 72539 (Figs 525–6), length 19·9 mm, width 33·0 mm; BB 72541 (Figs 530–1), length 20·3 mm, width 27·4 mm; loc. 20, colln O81, e.g. BB 72540 (Figs 528–9), length 18·5 mm; BB 72543 (Fig. 534). Loc. 11, Bancroft colln, e.g. BB 73928 (Fig. 533); loc. 20, Bancroft colln, e.g. BB 73913–4 (Figs 535, 538); loc. 31, e.g. BB 72538 (Fig. 527). Also recorded from locs 19, 26 and 30.

DISCUSSION. See p. 292.

Kjerulfina polycyma Bancroft
Figs 522, 523, 536, 537, 539–541

1929*a* *Kjerulfina polycyma* Bancroft : 61–62; pl. 2, figs 10–12.
1945 *Kjerulfina polycyma* Bancroft; Bancroft : 250–252; pl. 38, figs 1–5.
cf. 1952 *Kjerulfina* cf. *polycyma* Bancroft; Reed : 50; pl. 2, figs 6–7.
1957 *Kjerulfina limbata* Spjeldnaes : 156–157; pl. 9, figs 4, 9–10.
cf. 1977 *Kjerulfina* cf. *polycyma* Bancroft; Mitchell : 100–101; pl. 21, figs 7–10.
1978 *Kjerulfina polycyma* Bancroft; Harper & Boucot : pl. 14, figs 1–3, 5–9, *non* figs 4, 12.

DESCRIPTION. Plano-convex to gently concavo-convex ventrally geniculate *Kjerulfina*, elongately semicircular in outline, 65% as long as wide, occasionally larger individuals with an alate hinge line, pedicle valve initially gently convex, 12% as deep as wide, valve abruptly geniculate ventrally and trail 30% as long as valve is wide, disc semicircular in outline and surface covered with strong persistent rugae, ventral interarea apscaline with supra-apical foramen, pseudodeltidium appearing absent, dorsal interarea apscaline and with small vestigial arched chilidium; radial ornamentation unequally parvicostellate and often with median rib thickened and commonly with 5 ribs per mm, 10 mm anterior of the dorsal umbo.

Ventral interior with very short thickened teeth dividing angle between hinge and short receding dental plates which support them and extend forward for 10% of the valve length, ventral muscle field subquadrate, flabellate, and surrounded laterally by muscle-bounding ridges extending forward from dental plates and 85% as wide as long and extending forward for 40% of the length of the valve, median lanceolate adductor scars defined by small ridges and surrounded anteriorly by diductor tracks.

Dorsal interior with moderately strong, splayed, bilobed cardinal process ankylosed posteriorly to thin weakly divergent socket ridges which reach anteriorly for 12% of the length of the brachial valve, notothyrial platform moderately developed and anchor-shaped, median ridge fine.

DIMENSIONS.	length	width
Internal mould of pedicle valve, BB 9148, lectotype	–	–
Internal mould and cast of pedicle valve, BB 73908	23·6	34·5
Internal mould of pedicle valve, BB 73895	21·5	32·2
Internal mould of pedicle valve, BB 73887	22·6 (est.)	26·5 (est.)
Internal mould of brachial valve, BB 73901	23·9	31·0
External mould of pedicle valve, BB 73897	19·7 (est.)	38·2 (est.)

HORIZON AND LOCALITIES. All figured specimens are from the Bancroft collection in the BM(NH). BB 73908 is from loc. 28; the rest are from loc. 25. Also recorded from loc. 22.

DISCUSSION. Bancroft (1929*a*, 1945) distinguished between *K. trigonalis* and *K. polycyma* on the basis of rugae, ventral disc, axis of geniculation, posterolateral wings and ventral muscle area. He considered *K. trigonalis* to have finer discontinuous rugae, a flat as opposed to a uniformly convex ventral disc, a narrow and rounded as opposed to a wide, steep and abruptly angulate geniculate border. He thought that *K. polycyma* did not develop alae (independent wings) and supposedly had a shorter and relatively wider ventral muscle field, bounded by finer ridges.

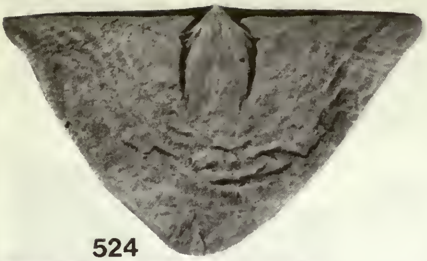
The present study indicates that *K. trigonalis* does indeed have much finer, more discontinuous rugae. However, a population of *K. polycyma* exhibits striking variation and a few individuals have rugae scarcely stronger than *K. trigonalis* (see Bancroft 1945 : 250). There is no obvious consistent difference in the convexity of the ventral disc. As regards the geniculate borders, *K. polycyma* populations do have consistently wider, steeper and more angulate trials. Alae seem to be persistently present in *K. trigonalis*, but occur only occasionally in *K. polycyma*. Perhaps the most striking difference between the two species is concerned with the ventral muscle field and cardinalia. *K. polycyma* has a consistently wider muscle area giving the whole field a quadrate appearance, but has weaker bounding ridges. Its teeth are stubbier and displayed at a more acute angle to the hinge axis than in *K. trigonalis*. Further, the dental plates are weaker and displayed at a wider angle. The notothyrial platform of *K. polycyma* is more strongly developed and its external ribbing appears to be slightly finer.

Spjeldnaes (1957) erected *K. limbata*, noting that it was closely related to *K. polycyma* but differed in terms of size and ventral muscle impression. Size is an unreliable taxonomic character and the ventral muscle configuration and impression are accommodated within the range of variation of *K. polycyma*; thus *K. limbata* is treated as a junior synonym of *K. polycyma*.

Holtedahl (1916) described *Strophomena brøggeri*, which Spjeldnaes (1957) referred to *Kjerulfina* (see also Bancroft 1945 : 250). In every respect *K. broeggeri* resembles *K. polycyma* except that *K. broeggeri* develops dorsal geniculates as well as ventral ones (see remarks in Spjeldnaes 1957 : 159). Obviously the species is in need of revision as it may not be a *Kjerulfina*, since no evidence of such variability has been found in the Salopian species.

Harper & Boucot (1978) suggest that *Kjerulfina* is possibly ancestral to the Strophonellidae. In support they illustrate several specimens which they assign to *K. polycyma* (Harper & Boucot 1978 : pl. 14). Two of these (pl. 14, figs 4, 12) are best assigned to *K. trigonalis*, but their locality description is inadequate to locate their stratigraphical position accurately. The remaining figured specimens are *K. polycyma* from localities used in the present study.

Figs 524–541 *Kjerulfina trigonalis* Bancroft, internal moulds of pedicle valves: 524 = lectotype BB 73834, ×1·5, 525 = BB 72539a, ×0·9, 527 = BB 72538, ×1·2, 528 = BB 72540a, ×1·5, 530 = BB 72541a, ×0·9; internal moulds of brachial valves: 532 = BB 72542, ×1·2, 533 = BB 73928, ×2, 534 = BB 72543, ×1·5, 535 = BB 73913, ×1·5; external moulds of pedicle valves: 526 = BB 72539b, ×1·2, 529 = BB 72540b, ×1·4, 531 = BB 72541b, ×1·1; external mould of brachial valve: 538 = BB 73914, ×1·3. *Kjerulfina polycyma* Bancroft, internal moulds of pedicle valves: 536 = lectotype BB 9148, ×1·5, 537 = BB 73895, ×1·3, 539 = BB 73887, ×1·4, 540 = BB 73908, ×1·5, 541 = cast from BB 73908, ×1·5.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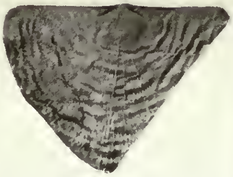
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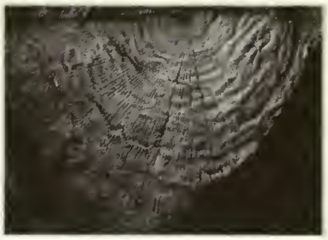
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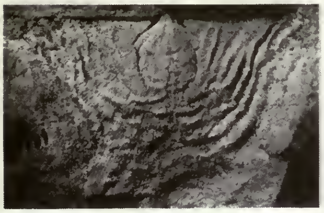
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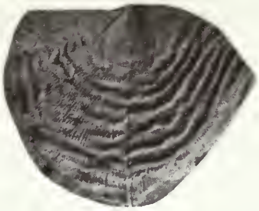
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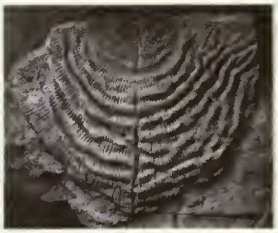
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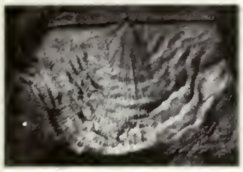
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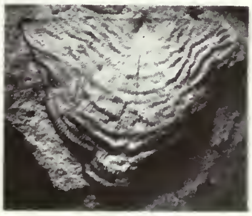
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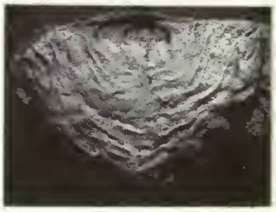
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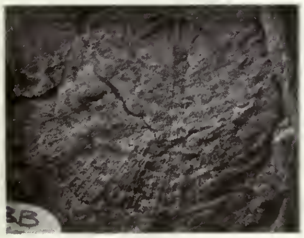
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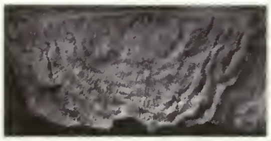
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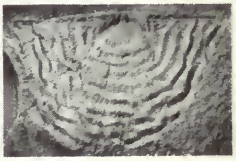
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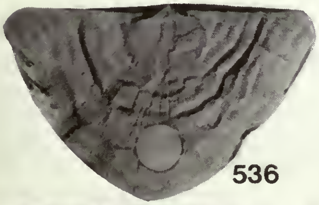
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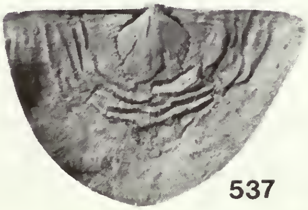
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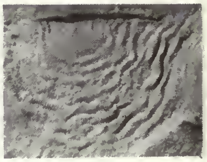
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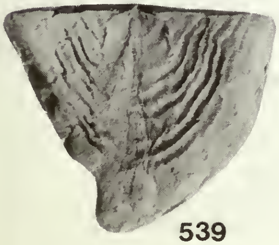
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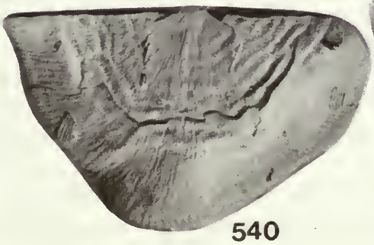
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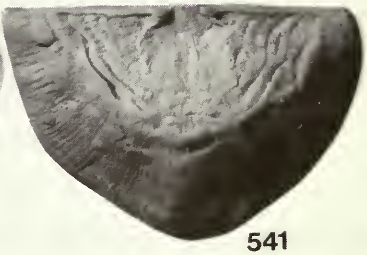
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Family **CHRISTIANIIDAE** Williams, 1953

Genus ***CHRISTIANIA*** Hall & Clarke, 1892

Christiania hollii (Davidson)

Figs 542–557

1871 *Strophomena Hollii* Davidson : 303; pl. 42, figs 18–19.
1958 '*Rafinesquina*' *holli* (Davidson) Dean : pl. 25, fig. 12.
1978 *Christiania hollii* (Davidson) Cocks : 123, 200.

DESCRIPTION. Semicircular to subquadrate concavo-convex *Christiania* with pedicle valve 75% as long as wide and 30% as deep as long and occasionally with sharp-sided sulcus, nature of delthyrium unclear but with apical foramen. Ornament of raised, sharp-sided, concentric ridges.

Ventral interior with impressed oval node containing muscle field and extending forward for about 50% of the valve length, elongate oval adductor track situated posteriorly and surrounded anteriorly by diductor track, dental plates very short and divergent.

Dorsal interior with thin, widely divergent socket ridges which lie parallel to hinge line, anterior to which is anchor-shaped protegular node. Outer pair of longitudinal septa separated and displaced slightly anterior of socket ridges, inner septa short and diverging at about 40°, nature of cardinal process unknown.

DIMENSIONS.	length	width
Internal mould of pedicle valve, BB 73610	1·4	1·8
Internal mould of pedicle valve, BB 73611	1·6	2·4
Internal mould of pedicle valve, BB 73612	1·6	2·2
Internal mould of pedicle valve, BB 73613	1·7	2·8
Internal mould of pedicle valve, BB 73614	1·9	2·6
Internal mould of brachial valve, BB 73620	1·7	2·5
External mould of brachial valve, BB 73623	1·6	2·1
External mould of brachial valve, BB 73624	1·4	2·3
External mould of pedicle valve, BB 73625	1·5	2·1

HORIZON AND LOCALITIES. Recorded from locs 50 and 51. All Davidson's type specimens are on a small block collected by Morris from loc. 51.

DISCUSSION. This peculiar brachiopod can be allocated to the genus *Christiania* on the basis of the brachial valve septa (Cocks 1978). *C. hollii* resembles the younger *C. portlocki* Mitchell from the Killey Bridge Formation of Pomeroy, Ireland (Mitchell 1977). The only obvious difference between the two species is that the young growth stages of *C. portlocki* have much finer concentric ornament. As no larger specimens of *C. hollii* exist it is difficult to compare the species any further.

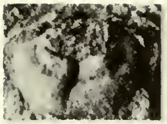
Family **LEPTAENIDAE** Hall & Clarke, 1894

Genus ***LEPTAENA*** Dalman, 1828

Leptaena salopiensis Williams

1963 *Leptaena salopiensis* Williams : 461–462; pl. 15, figs 7, 8, 10–16.

REMARKS. This species, described and figured by Williams (1963), is known from locs 35, 42–5 and 47 of the Acton Scott Formation.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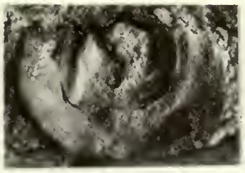
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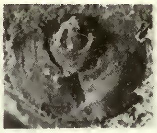
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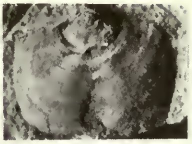
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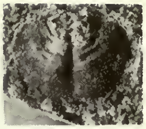
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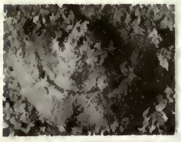
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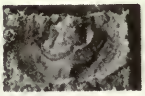
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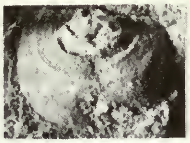
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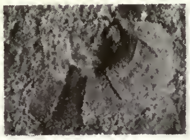
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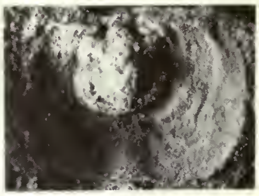
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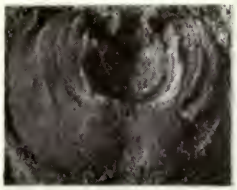
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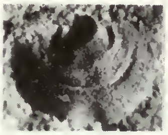
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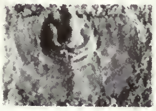
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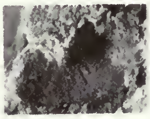
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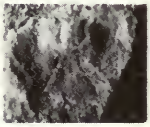
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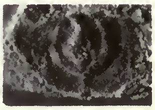
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Figs 542–557 *Christiania hollii* (Davidson), internal moulds of pedicle valves: 542 = BB 73612, ×8·4, 543 = BB 73613, ×10, 544 = BB 73616, ×8·3, 545 = BB 73614, ×8·5, 546 = BB 73610, ×9, 547 = BB 73615, ×8, 549 = BB 73611, ×9; internal moulds of brachial valves: 548 = BB 73622, ×8·5, 550 = BB 73619, ×10, 551 = BB 73620, ×11·6, 555 = BB 73618, ×9·5, 557 = BB 73621, ×9·2, 556 = BB 73617, ×9; external moulds of brachial valves: 552 = BB 73623, ×13·8, 554 = BB 73624, ×8·3; external mould of pedicle valve: 553 = BB 73625, ×9.

Order **SPIRIFERIDA** Waagen, 1883
Suborder **ATRYPIDINA** Moore, 1952
Superfamily **ATRYPACEA** Gill, 1871
Family **ATRYPIDAE** Gill, 1871
Subfamily **ZYGOSPIRINAE** Waagen, 1883

Genus ***ZYGOSPIRA*** Hall, 1862

? ***Zygospira*** sp.
Figs 516–521

Description. Small biconvex *Zygospira*, with a brachial valve 95% as long as wide and 20% as deep as long, and a pedicle valve 30% as deep as long; dorsal fold and ventral sulcus weakly developed, 35% as wide as the valve, rostrate with highly curved ventral umbo, radial ornamentation of rounded costae with up to 2 on the dorsal fold and 4 to 7 on the lateral slopes.

Ventral interior with very small teeth extending anteriorly for about 20% the length of the valve, muscle field unknown.

Dorsal interior with small, medially cleft triangular hinge plate; muscle scars not impressed.

Dimensions.	length	width
Internal mould of brachial valve, BB 72528	3·5	3·5
Internal mould of brachial valve, BB 72525	4·0	4·0
Internal mould of brachial valve, BB 72524	3·9	4·3
Internal mould of pedicle valve, BB 72523	3·3	–

Horizon and localities. BB 72528 from loc. 43, colln CP4. BB 72523, BB 72526 and BB 72525 from loc. 44, collns OA10, OA13 and OA14 respectively. BB 72524 from loc. 35, colln DH1 and BB 72527 from loc. 45, colln AS3. Also recorded from locs 42 and 46.

Discussion. Occasional disarticulated valves from the Acton Scott Formation are provisionally assigned to *Zygospira* on the basis of their hinge plate and valve configuration. However, the sulcal development is not reminiscent of *Zygospira*.

Acknowledgements

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